PLAY AND SOCIAL RELATIONSHIPS IN THE MEERKAT (*SURICATA SURICATTA*)

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I, the undersigned, hereby declare that the work contained in this dissertation is my own original work and that I have not previously, in its entirety or in part, submitted it at any university for a degree.

SUMMARY

Despite more than three decades of research, and the postulation of more than 30 hypotheses of function, the adaptive significance of play remains unknown. This study quantitatively evaluated a selection of hypotheses of function, using data collected from a wild population of small, social carnivore, the meerkat, *Suricata suricatta*. The study found that although play in meerkats carried an energetic cost, with individuals modulating their frequency of play in response to their energy intake, none of the hypotheses evaluated by the study could identify the adaptive benefits that meerkats derived from play. Play did not increase 'social harmony' by reducing aggression between playmates, nor did it strengthen an individual's bonds to its social group, such that it remained in the group for longer, or contributed more to the group's cooperative activities. There was no evidence that meerkats used play to strengthen alliances between individuals, and young meerkats played no more frequently with their future dispersal partners than with matched controls with which they did not disperse. Play fighting experience did not improve a meerkat's subsequent fighting skills, and individuals that ultimately won the dominant breeding position within a group (through serious fighting) played no more frequently, and no more successfully, as youngsters, than the littermates that they defeated in combat. Although play was inhibited by aggression, meerkats did not use play to contest, assert or establish dominance status, and there was little evidence to suggest that the preference young meerkats showed for play partners that were well matched in age, size and ability arose from their use of play for self-assessment.

This study assessed only those hypotheses of function that predicted benefits that were of importance to the inclusive fitness of the study species. For example, the enhancement of social harmony and group cohesion should be invaluable to a species whose survival is dependent upon social cooperation; and the high reproductive skew exhibited by this species places huge value upon fighting skill and the ability to win social dominance. As a consequence, this study's negative findings suggest strongly that play is not capable of providing these benefits, and that play behaviour is unlikely to be used for these purposes in any mammal species. I conclude that the most likely function of play (based on play's ubiquitous characteristics, and the findings of neurological research on rats) is the promotion of growth of the cerebral cortex.

OPSOMMING

Ten spyte van meer as drie dekades van navorsing en die voorstelling van meer as 30 hipoteses oor funksie, bly die aanpassingswaarde van spel onbekend. Hierdie studie is 'n kwantitatiewe evaluasie van verskeie hipoteses oor funksie, en gebruik data versamel vanuit 'n wilde bevolking van 'n klein sosiale karnivoor, die meerkat, *Suricata suricatta.* Die studie het bevind dat hoewel spel in meerkaaie 'n energetiese koste beloop, met individue wat hul spelfrekwensie aanpas by energie-inname, geen-een van die hipoteses onder beskouing die aanpassingswaarde van spel vir meerkaaie kon verduidelik nie. Spel het nie "sosiale harmonie" bevorder deur die afname in aggressie tussen speelmaats nie, en het ook nie 'n individu se verbintenis tot sy sosiale groep versterk sodat hy langer in die groep sou bly of meer sou bydra tot samewerkingsaktiwiteite nie. Daar was geen bewyse vir die gebruik van spel in die versterking van bondgenootskappe tussen individue nie, en jong meerkaaie het nie meer gereeld met toekomstige verspreidings-venote gespeel as met gepaarde kontroles saam met wie hulle nie uiteengegaan het nie. Speelse gevegte het nie 'n meerkat se daaropvolgende gevegsvermoëns verbeter nie, en die individue wat uiteindelik die dominante voortplantingsposisie in 'n groep gewen het (deur ernstige stryd) het nie meer gereeld of meer suksesvol as jongelinge gespeel in vergelyking met die werpselmaats wat hulle in die stryd oorwin het nie. Hoewel spel deur aggressie onderdruk is, het meerkaaie spel nie gebruik om dominante range te beveg, bevestig of tot stand te bring nie. Daar was min bewyse ter ondersteuning van die voorstel dat jong meerkaaie se voorkeur vir speelmaats wat hul gelyke is in ouderdom, grootte en vermoë, onstaan het in die gebruik van spel vir selfondersoek.

Hierdie studie het slegs die hipoteses van funksie beskou wat voorspellings gemaak het oor die voordele wat belangrik is in die inklusiewe fiksheid van die studie-species. Byvoorbeeld, die verbetering van sosiale harmonie en groepsamehang behoort van onskatbare waarde te wees vir 'n species wat afhanklik is van sosiale samewerking vir oorlewing; en die hoë graad van voorkeuraanwas duidelik in hierdie species plaas groot waarde op gevegsvaardighede en die vermoë om sosiale dominansie te wen. Gevolglik dui hierdie ondersoek se negatiewe bevindinge daarop dat spel nie hierdie voordele kan bied nie, en dat speelgedrag heel waarskynlik nie vir hierdie doeleindes in enige soogdier-species gebruik word nie. Ek kom tot die gevolgtrekking dat die heel waarskynlikste funksie van spel (gebaseer op spel se alomteenwoordige kenmerke en die bevindinge van neurologiese navorsing op rotte) die bevordering van groei in die serebrale korteks is.

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CHAPTER ONE

GENERAL INTRODUCTION

1.1 WHAT IS PLAY?

1.1.1 Defining play

While play behaviour in most mammal species is readily recognizable by both professional ethologist and layman alike, the development of an acceptable definition of play has proven contentious and difficult (Lorenz 1956; Hinde 1970; Bekoff & Byers 1981; Fagen 1981; Martin 1984a). Unlike most behaviour patterns, which are easily defined by their function or consequences (e.g. predatory behaviour, mating, aggression), play's function is currently not known. As a consequence, attempts have been made to define play by its structural characteristics (Loizos 1967, Fagen 1981), but this is problematic; firstly, because of the diversity of play behaviour shown by different taxa; and, more importantly, the motor patterns adopted during the play in a particular species often appear, at least at a superficial level, to be the same as those used in serious functional contexts. Under these circumstances, simple descriptions of motor acts are clearly inadequate, and some reference to functional context must be made. Although the problem has not been fully resolved, most ethologists now accept a definition of play that melds both structural and functional elements, such as that presented by Martin & Caro (1985):

> 'Play is all locomotor activity performed postnatally that appears to the observer to have no obvious immediate benefits for the player, in which motor patterns resembling those used in serious functional contexts may be used in modified form. The motor acts constituting play have some or all of the following structural features: exaggeration of movements, repetition of motor acts, and fragmentation or disordering of sequences of motor acts.'

Play behaviour is also traditionally divided into the following subcategories: 'Social play' - play directed at conspecifics (e.g. pouncing, grabbing, inhibited biting, wrestling, butting, mounting, chasing); 'object play' - play directed at inanimate objects (e.g. tugging, carrying, tossing, shaking and manipulating); and 'locomotor play' - apparently spontaneous movements that carry the player around its environment (e.g. running, leaping, jumping, dangling, rolling, somersaulting). These categories are not necessarily mutually exclusive.

1.1.2 Is 'play' a valid category of behaviour?

It has been suggested that the concept of 'play' is misleading and redundant, because the behaviour that we perceive as play is simply immature behaviour (for example, play-fighting is just an immature form of real fighting). The proponents of this view (Welker 1971; Lazar & Beckhorn 1974) suggest that it would be more profitable to study the ontogenetic processes for particular behaviours in their own right (e.g. the ontogeny of aggressive behaviour), rather than lumping 'immature' behaviour into the meaningless and artificial category of 'play'. It has also been suggested (Lorenz 1956; Leyhausen 1978) that play is simply a by-product of motivational anomalies, as, for example, is the displacement grooming shown by frightened rodents (Fentress 1968).

There is, however, strong evidence to suggest that play behaviour is not simply an immature version of adult behaviour. Detailed study has revealed that play-fighting is structurally distinct from real fighting in many species of carnivore (Henry & Herrero 1974; Hill & Bekoff 1977; Poole 1978), primate (Stevenson 1978; Owens 1975b; Symons 1978b) and rodent (Pellis & Pellis 1998), and that these differences are maintained even after serious forms of agonistic behaviour have developed. In fact, in the ontogeny of a number of species - e.g. coyotes, *Canis latrans* (Bekoff 1974), spotted hyenas, *Crocuta crocuta* (Drea et al. 1996), collared peccaries, *Dactyles tajacu* (Byers 1984), and domestic pigs, *Sus scrofa* (McBride 1963) - mature forms of aggressive behaviour appear prior to the appearance of play. The widespread existence of specific 'play-soliciting signals' - e.g. the play-bow of canids (Bekoff 1977c) and lions, *Panthera leo* (Schaller 1972), the open-mouthed play-face of primates (Aldis 1975; Owens 1975b; Stevenson 1978; Symons 1978b), the play pheromone of voles, *Microtus agrestis* (Wilson 1973), and the play vocalization of dwarf mongooses, *Helogale undulata rufula* (Rasa 1984) - also supports the view that play is a distinct category of behaviour. Similarly, the fact that play deprivation produces a play-specific rebound effect (Chepko 1971; Baldwin & Baldwin 1974; Oakley & Reynolds 1976; Panskepp & Beatty 1980) is clear evidence that play is motivationally distinct, and not simply an epiphenomena of other behaviour patterns.

While few biologists now question the authenticity of play as a class of behaviour in its own right, there is growing evidence to suggest that play may not be a homogeneous category

(Rosenburg 1990; Burghardt 1998), and that the different modes of play (social, object or locomotory) may differ in their origin, ontogeny, proximate cause or function (Breuggeman 1978; Fassino 1982). For example, social, object and locomotor play have different developmental profiles in domestic cats, *Felis catus* (Barrett & Bateson 1978; Mendoza & Ramireza 1987), Cuvier's gazelles, *Gazella cuvieri* (Gomendio 1988), olive baboons, *Papio anubis* (Chalmers 1980), South American fur seals, *Arctocephalus australis* (Harcourt 1991a), and cheetahs, *Acinonyx jubatus* (Caro 1995). Similarly, rates of social and object play are affected differently by early weaning (Martin & Bateson 1985b) or social isolation in domestic cats (Guyot, Bennett & Cross 1980), or by injections of gonadal hormones in bonnet macaques, *Macaca radiata* (Rosenblum & Bromley 1978). While this suggests that different components of play may be motivationally distinct, 'play' is still considered a valid behavioural categorization by most researchers since all play shares common features (Fagen 1981; Burghardt 1984) and there are often no clear boundaries between types of play within the play bouts of most species (Thompson 1998; Spinka et al. 2001).

1.1.3 Phylogenetic distribution of play

Play occurs in all mammalian orders, and appears to be ubiquitous in carnivores, pinnepeds, primates and ungulates (Fagen 1981; Smith 1982). Because of this widespread distribution, it is believed that play has a long phylogenetic history, most likely originating with the earliest mammals, around 70 million years ago (Byers 1984).

Within some mammalian orders (such as Rodentia), the extent of play behaviour varies greatly between species; for example, social play is highly developed in *Rattus norvegicus,* but virtually non-existent in *Mus musculus* (Poole & Fish 1975). Pellis & Iwaniuk (1999) found that this interspecific variation within Rodentia was not related to phylogeny. The distribution of play among marsupial families is positively correlated with cerebral development (Byers 1999), and a similar relationship appears to exist in birds (Ortega & Bekoff 1987), in which play has been observed in two orders (Psittaciformes and Passeriformes - Ficken 1977). There is also possibly some evidence of object play occurring in turtles (Burghardt 1998).

1.1.4 Ontogenetic distribution of play

Play occurs most frequently in juvenile mammals (Fagen 1981, Smith 1982; Byers & Walker 1995; Byers 1998). It normally appears at low rates early in postnatal life, then rises to a peak at approximately late lactation (or at the onset of solid food consumption – Barber 1991) before declining prior to sexual maturity (e.g. Espmark 1971; Baldwin & Baldwin 1974; West 1974; Pratt & Anderson 1979; Chalmers 1980; Bekoff & Byers 1981; Muller-Schwarze 1984; Martin & Bateson 1985a; Miller & Byers 1991). Secondary peaks (often seasonal) may occur in some species, such as gray squirrels, *Sciurus carolinensis* (Horwich 1972), baboons (Cheney 1978), and domestic sheep, *Ovis aries* (Sachs & Harris 1978), but play is rare in adult animals (Aldis 1975; Fagen 1981), although many species play with their own offspring. Species that hunt cooperatively, such as lions (Schaller 1972), wild dogs, *Lycaon pictus*, and timber wolves, *Canis lupus* (Mech 1970), also indulge in social play prior to foraging, and adult play is known to be common in domestic rats (Adams & Boyce 1983), polar bears, *Ursus maritimus* (Latour 1981), North American river otters, *Lutra canadensis* (Beckel 1991), spotted hyenas (Kruuk 1972), domestic cats (Hall 1998) common marmosets, *Callithrix jacchus jacchus* (Stevenson & Poole 1982) and mountain hares, *Lepus timidus* (Flux 1970).

1.2 DOES PLAY HAVE A FUNCTION?

> 'The amount of time and paper spent on speculation on possible functions of motor play in immature animals is in inverse proportion to the amount of facts available on this question.'
>
> Muller-Schwarze - **1971**

> 'Quite simply, the functions of play behavior are not known.'
>
> Martin & Caro - **1985**

> 'Why and how has play behavior evolved and how has it been maintained...? There has been little success in achieving a generally valid and empirically supported answer to these questions.'
>
> Spinka, Newberry & Bekoff - **2001**

Despite more than three decades of research, and the postulation of more than 30 hypothesis of function (Baldwin & Baldwin 1977), the adaptive significance of play remains unknown. Is it possible that play simply does not have an adaptive function; after all, one of play's defining characteristics (see Section 1.1) is that it has 'no obvious immediate benefits to the player'? While the mere existence of a behaviour in a natural population is often taken as evidence that it serves an adaptive role, this is not necessarily the case (Hinde 1975). Play could simply be a behavioural vestige - once adaptive in the phylogenetic history of the species, but currently without fitness effects. While the widespread prevalence of play in mammalian taxa, and the existence of taxa-specific play-soliciting signals, suggest that play is being actively maintained by natural selection and is not just a product of phylogenetic inertia, the argument that play is vestigial can only be refuted by evidence that play carries a significant fitness cost for the player.

1.2.1 Is play costly?

For decades biologists accepted, without question, the assumption that play was a costly activity (e.g. Beach 1945; Berlyne 1966; Loizos 1966, 1967; Farentinos 1971; Bekoff 1972; Poirier & Smith 1974; Symons 1974; Poole & Fish 1975; Berger 1980; Bateson & Young 1981; Byers 1981; Fagen 1981; Smith 1982). Young mammals clearly devoted time and energy to play - time and energy that could have been invested in growth, survival or reproduction. However, the growing realization that empirical data for play's costliness did not exist (Bekoff & Byers 1981; Martin 1982; Martin & Caro 1985), led to a number of attempts to quantify investment in play. As a result, we know that young mammals devote only a small percentage of their time budget to play: for example, domestic kittens spend 9% of their day playing (Martin 1984b), cheetahs 3% (Caro 1995), lions 2-6% (Schaller 1972), coyotes 1% (Bekoff & Wells 1986), pronghorn, *Antilocapra americana*, 1-2% (Miller & Byers 1991), red colobus, *Colobus badius*, 3-14% (Clutton-Brock 1974), chacma baboons, *Papio cynocephalus*, 3-5% (Cheney 1978), olive baboons 3-20% (Rose 1977; Nash 1978), and rhesus macaques, *Macaca mulatta*, 1-6% (Levy 1979). This also translates into a relatively low energetic investment, with domestic kittens devoting 4-9% of their daily energy expenditure to play (Martin 1984b), domestic rats 2-3% (Siviy & Atrens 1992), white-tailed deer, *Odocoileus virginianus*, 1% (Muller-Schwarze et al. 1982) and pronghorns 2% (Miller & Byers 1991).

While some authors (Martin & Caro 1985, Barber 1991) have suggested that this level of energy expenditure is trivial and carries no real fitness cost, others argue that apparently small energetic investments may not be small from a selective viewpoint (Miller & Byers 1991; Bekoff & Byers 1992). Miller and Byers (1991), for example, showed that while pronghorn fawns devote only 2% of their total energy budget to play, this equates to 20% of their energy expenditure, after the costs of resting metabolic rate and growth are removed. They calculated that if a pronghorn fawn diverted the energy it expended on running play into growth, it would gain an additional 7% of its mass by weaning.

It has also been proposed (Martin & Caro 1985) that the tendency for animals to forgo play when suffering extreme food shortage (Southwick 1967; Loy 1970; Baldwin & Baldwin 1974) supports the tenet that play is energetically costly, because energetically stressed organisms should curtail those behaviours that cost the most. However, there is only limited evidence that play responds to fluctuations in energy consumption under non-life threatening conditions, and while a number of field studies have found a positive correlation between quality of diet (or habitat quality) and rates of play (Geist 1971; Lee 1984; Barrett et al. 1992, Sommer & Mendoza-Granados 1995), the causality of the relationship has not been established. In fact, there is good evidence to suggest that it is the accessibility of food (and consequent changes in the amount of time individuals must devote to foraging) that affects play, rather than energetic factors (Baldwin & Baldwin 1976; Muller-Schwarze et al. 1982). Nunes et al. (1999) also came to this conclusion, after monitoring play and foraging behaviour in experimentally provisioned Belding's ground squirrels (*Spermophilus beldingi*).

Of course, energy expenditure is not the only potential cost of play. Many researchers have reported survivorship costs, although quantitative assessment of these costs has generally not been undertaken. Playing individuals suffer an increased risk of injury, or death, from falls (bighorn sheep, *Ovis canadensis*, Welles & Welles 1961; chimpanzees, *Pan trogodytes*, van-Lawick-Goodall 1968; Siberian ibex fawns, *Capra ibex sibirica*, Byers 1977) or by becoming trapped in mud (elephants, *Loxodonta africana*, Douglas-Hamilton & Douglas-Hamilton 1975), impaled on cacti (bighorn sheep, Berger 1980), washed out to sea (Galapagos fur seals, *Arctocephalus galapagoensis*, Arnold & Trillmich 1985), or separated from their mother (chimpanzees and Japanese macaques, *Macaca fuscata*, Fagen 1981; bighorn sheep, Berger 1980). Playing animals also tend to suffer higher rates of predation, because play both distracts the player and is conspicuous to predators (vervet monkeys, *Cercopithecus aethiops*, Hausfater 1976; Thompson gazelles, *Gazella thompsonii*, Caro 1988; South American fur seals, Harcourt 1991b). The survivorship costs of play can be surprisingly high, for example, although South American fur seal pups devote only 6% of their time to play, 85% of the 26 pups that Harcourt (1991b) saw predated by sea lions, were playing at the time they were captured. Play may also have indirect survivorship costs, for example, play in cheetah cubs reduces the hunting success of their mother by alerting the prey and in Caro's study (1987) play was responsible for 9% of failed hunts.

1.2.2 One function or many?

The search for a single, all-encompassing function for play behaviour may, of course, be an inappropriate quest. Even if play evolved just once in the phylogenetic history of mammals (Byers 1984; Barber 1991) - and some authors dispute this assumption (Pellis 1988) - it seems likely that play behaviour may have developed different functions in different taxa, during its long phylogenetic history (Suomi 1982). Byers (1984) evocatively likened the diversification of play in mammals to that of the mammalian pentadactyl forelimb: while the basic five-digit design has been maintained, the limb's original function (walking) has been diversified to include digging, flying, running, swimming, etc. Although this multi-functionary approach may explain why decades of research has failed to identify a single, unifying function for play in all taxa, it does not explain our failure to obtain clear, indisputable evidence of an adaptive function for play in *at least* a single species (Martin & Caro 1985; Spinka et al. 2001).

1.3 PROPOSED FUNCTIONS OF PLAY

Numerous hypotheses have been advanced to explain the adaptive significance of play. They are presented here grouped into six main categories.

1.3.1 Social skills

This set of hypotheses is founded on the premise that individuals learn about one another during play. The social skills set of hypotheses suggest that play:

- teaches a young mammal how to recognize and relate to members of its own species (Vandenberg 1982), allowing an individual to learn how to develop general affectational ties with conspecifics (Harlow & Harlow 1966);
- teaches individuals to recognize, and become familiar with, group members (Bekoff 1978; Gomendio 1988; Pellis & Pellis 1992), thus avoiding the often very unpleasant consequences of being perceived as an outsider (e.g. Barnett 1958; Bernstein 1964);

- teaches individuals to recognize, and become familiar with, their kin (Bekoff 1978), assisting in long-term kin recognition (especially important in solitary species that may reencounter siblings after dispersing);
- helps individuals to learn, refine and practice social communication skills (Mason 1965; Dolhinow 1971; Jolly 1972; Poirier & Smith 1974);
- teaches individuals complex social skills (Baldwin & Baldwin 1974; Humphreys & Einon 1981), such as the accurate appraisal of another's mood or motivation (Bekoff & Allen 1998).

The strongest evidence in support of the 'social skills' hypotheses comes from social deprivation experiments which show that rhesus macaques, rats and cats reared without peers react inappropriately to conspecifics, exhibiting unusually high levels of timidity and/or aggression (Mason 1961; Harlow & Harlow 1969; Lore & Flannelly 1977; Guyot et al. 1980). Social-deprivation appears to affect the individual's basic communicative skills (Mason 1961), as it has been shown experimentally that peer-deprived rhesus macaques are unable to interpret the facial expressions of conspecifics (Miller, Caul & Mirsky 1967) and make inappropriate facial expressions themselves, such as staring (a threatening gesture) at dominant animals (Mitchell 1972). There is some evidence that social play teaches young animals these basic communication skills, as young macaques denied the opportunity to play (regardless of whether they were reared without peers, reared with peers that were incompetent play partners, or prevented from playing by their mothers or other adults) show this same hyper aggressiveness (Suomi 1979). Similarly, the detrimental effect of social isolation on young rats (hyper or hypo defensiveness) can be prevented by exposing them to one hour of play experience daily (Potegal & Einon 1989). Rats exposed to a drugged social partner that did not play, showed few behavioural differences from completely isolated rats (Einon et al. 1978).

Unfortunately, these results cannot be considered conclusive since deprivation experiments are highly prone to confounding variables (Bekoff 1976; Martin & Caro 1985). The drugged rats in Einon et al.'s study, for example, presumably behaved differently from normal rats in more ways than just playfulness. A cautious interpretation of this data is also encouraged by studies on free-ranging primates, in which reductions in social play (brought about by food shortage or poor habitat quality) had no apparent effect on social relationships (Baldwin & Baldwin 1974; Lee 1984). Symons (1978b) argues convincingly that young rhesus macaques do not use social play to learn appropriate responses to signals of aggression and submission (such as the facial expressions documented by Mitchell (1972)) for the simple reason that these signals do not occur during play! He does concede, however, that play may teach youngsters to look at faces for meaningful social signals.

While there is good evidence (Owens 1975a; Breuggeman 1978; Symons 1978a) that primates do *use* play in socially complex ways to manipulate one another (e.g. subadult female baboons play with the infants of high-ranking mothers in an attempt to cultivate alliances with these females (Cheney 1978), and chimpanzees use play to distract infants from weaning (van Lawick-Goodall 1968), this does not mean that play's primary function is the learning of complex social skills.

It has been argued that if the 'social skills' hypotheses were valid, interspecific variation in the frequency of play should be positively correlated with sociality, and play should not occur in solitary species (Smith 1982). Despite early suggestions that play and sociality were positively related (Altmann 1963; Poirier & Smith 1974; Bekoff 1977a), there is now good evidence that this is not the case, at least for canids and rodents (Biben 1983; Pellis & Iwaniuk 1999). However, a number of authors have questioned the validity of Smith's argument (Bekoff 1982; Burghardt 1982), claiming that even solitary species take part in complex, and important, social interactions (e.g. Leyhausen 1965), and that attempting to designate a 'species-typical' level of sociality is meaningless, since intraspecific variation in social organization is so widespread.

Smith (1982) also suggested that the 'social skills' hypotheses failed to account for the fact that males play more frequently than females in many species, particularly primates - e.g. chimpanzees (van Lawick-Goodall 1968), old world monkeys (Kummer 1968; Bertrand 1969; Seay et al. 1972; Simonds 1977; Symons 1974; Owens 1975a; Hrdy 1977; Wolfheim 1977; Raleigh et al. 1979), squirrel monkeys, *Saimiri sciureus* (Baldwin & Baldwin 1974), common marmosets (Abbott 1978), Norway rats (Meaney & Stewart 1981), golden hamsters, *Mesocricetus auratus* (Goldman & Swanson 1975), domestic sheep (Sachs & Harris 1978), and stellar sea lions, *Eumetopias jubata* (Gentry 1974). However, social deprivation experiments with rhesus macaques (Sackett 1974) have revealed that males are more severely affected by isolation than females, possibly reflecting a greater need in males to learn basic social skills, and potentially accounting for their increased levels of play.

In conclusion, the evidence relating to the 'social skills' hypothesis is insufficient to allow the hypothesis to be either accepted or dismissed.

1.3.2 Social bonding

This set of hypotheses is founded on the premise that play encourages an individual to 'like' its playmates, thereby strengthening social ties and reducing aggression. The social bonding set of hypotheses suggest that play:

- socializes general aggressive tendencies (Ghiselin 1974; Suomi 1982);
- reduces aggression and increases 'friendship' between group members or littermates, allowing them to live together amicably (West 1974; Poole 1978; Pellis & Pellis 1992; Drea et al. 1996; Soderquist & Serena 2000);
- creates friendships and alliances that facilitate future co-operation - e.g. between future dispersal partners, philopatric daughters, etc. (Berman 1982; Smith 1982; Waterman 1986);
- increases an individuals' ties to its social group, strengthening group cohesion and delaying dispersal (Poirier & Smith 1974; Bekoff 1977b, 1982; Gaines & McClenaghan 1980; Baldwin 1982; Byers 1984);
- reduces hostility and promotes affiliative behaviour in members of the opposite sex, thus enhancing reproductive opportunities through mate choice and sexual selection (Ghiselin 1974, 1982)
- allows dominance hierarchies to be established or maintained without aggression (Carpenter 1934; Dolhinow 1971; Poirier & Smith 1974; Geist 1978; Berman 1982; Paquette 1994).

Unfortunately, little attempt has been made to test the 'social bonding' set of hypotheses, despite their widespread popularity. Drea et al. (1996) found that rates of social play in captive, infant spotted hyaenas rose steadily as rates of sibling aggression fell, peaking at the age at which the cubs would normally integrate with others in the pack. They concluded that social play contributed to the termination of serious aggression and promoted social cohesion in this species. Holmes (1995), working with captive golden-mantled ground squirrels (*Spermophilus literalis*), found a negative relationship between the frequency of play and agonism when comparing interactions between littermates and non-littermates, and Wilson (1973), in a study of captive voles, found that autumn-born males - which did not play - were aggressive at sexual maturity, while spring-born males - which played extensively - remained tolerant of male conspecifics. However, Watson (1993) found no relationship between rates of aggression and social play in captive red-necked wallabies, *Macropus rufogriseus banksianus*.

In solitary carnivorous species, such as polecats, *Mustela putorius,* (Poole 1978), domestic cats (West 1974) and chuditch, *Dasyurus geoffroii,* (Soderquist & Serena 2000), rates of play in captive individuals decline markedly at the age at which littermates disperse in the wild, suggesting that play may serve to reduce the hostility that these animals normally exhibit toward conspecifics, allowing young littermates to cohabit without inflicting injury upon one another. In fact, Soderquist & Serena (2000) suggest that this hypothesis can also explain the phylogenetic distribution of play in Dasyurids - in which larger species play extensively while those weighing less than 100g do not play at all (Byers 1999). They suggest that the young of larger species are capable of inflicting serious injury on one another and thus need to play, while those of smaller species cannot inflict harm so do not need to play.

The hypotheses that suggest that play enhances friendships, alliances or group cohesion - theoretically by providing strong positive social conditioning (Baldwin 1982) - are supported only by a few anecdotal observations of macaques. Sugiyama (1976), for example, observed 'a few instances' of playmates dispersing together in Japanese monkeys, and young male rhesus monkeys, transferring into new groups, initially establish relationships with males they once knew (and hence played with) in their natal group (Boelkins & Wilson 1972; Hausfater 1972). Although involvement in non-agonistic social interactions, such as allogrooming, may influence an individual's decision to disperse (Harcourt & Stewart 1981; Harris & White 1992), it is not known whether play has this effect.

The hypothesis that play assists in the establishment, or maintenance, of rank order is lent some credence by the finding that the roles adopted during play often reflect social dominance relationships (e.g. Owens 1975b; Bekoff & Wells 1986; Pellis & Pellis 1992; Biben 1998). However, play and periods of dominance competition do not tend to overlap ontogenetically (Smith 1982), as would be expected if play was used to establish rank, with most species either curtailing play at the onset of rank-associated agonistic interactions (e.g. rhesus macaques, Symons 1978b; Norway rats, Panskepp 1981; Cuvier's gazelle, Gomendio 1988) or establishing dominance rank prior to the appearance of play (e.g. coyotes, Bekoff 1974; collared peccaries, Byers 1984; spotted hyaenas, Drea et al. 1996). In fact, anecdotal observations suggest that aggressive interactions act as a strong inhibitor of play (Joslyn 1973; Meier & Devanney 1974; Symons 1978b; Taylor 1980; Stevenson & Poole 1982; Thompson 1998).

Although Paquette (1994) found some evidence that adolescent chimpanzees may use play to challenge dominance relationships, his study was restricted to four captive individuals whose play fights routinely escalated into real aggression. Symons (1978a), by contrast, found that rank-reversals in free-ranging rhesus macaques did not derive from play, and only individuals not actively competing for status engaged in play. He argues convincingly that play fights could not be used to establish rank and still remain playful, because individuals would have to react to play initiations as they would to a threat or challenge (i.e. with either submission or escalation). Further evidence against the hypothesis is provided by Baldwin & Baldwin's (1974) finding that dominance relationships in a group of squirrel monkeys that did not play (due to a scarcity of food) appeared normal. In a similar vein, species in which dominance rank is fixed by maternal status play just as frequently as species in which rank is mutable by physical contest (Smith 1982).

1.3.3 Practice of motor skills

This very popular hypothesis (Groos 1898; Symons 1978b; Fagen 1981; Smith 1982; Caro 1988) states that animals use play to practice motor skills needed in adulthood. The practice hypothesis claims that play provides individuals with a safe opportunity to practice and refine their:

- fighting skills (Symons 1978b; Byers 1980; Pellis 1981; Jamieson & Armitage 1987; Watson & Croft 1993; Miller & Byers 1998);
- predatory skills (Egan 1976; Leyhausen 1979; Biben 1982b; Martin 1984a);
- predator-avoidance behaviour (Ewer 1966; Wilson & Kleiman 1974; Smith 1982; Gomendio 1988; Hass & Jenni 1993)
- mating behaviour (Groos 1898; Moore 1985)

Although this hypothesis is one of the few to have been systematically tested, supportive evidence is basically limited to arguments concerning the structural design of play. Play fighting, for example, appears to be very similar to real fighting in many species (e.g. Poole 1966; Barash 1973; Gentry 1974; Owens 1975b; Symons 1978b) thus making it optimal for the practice of fighting skills (Smith 1982). Other examples of arguments of 'optimal design' (Martin & Caro 1985) include the fact that the males of many species engage in both more serious fighting and more play fighting than the females (e.g. Symons 1978b; Berger 1980;

Byers 1980; Biben 1982a; Meaney et al. 1985; Pfeiffer 1985; Crowell-Davis et al. 1987; Watson & Croft 1993), and interspecific differences in 'serious' adult behaviours are often reflected in equivalent interspecific differences in play (e.g. Bekoff 1974; Biben 1982b; Caro & Alawi 1985). However, as noted by Ghiselin (1982), one would expect animals to engage only in the sorts of behaviour that are characteristic of their species and sex, so a mere correlation between what an animal does in play and what it does in 'serious' activities provides minimal evidence of practice.

Detailed analyses of the motor patterns used in play have also revealed that the resemblance between play and 'serious' behaviour patterns are often only superficial. During play fighting, for example, the specific targets of attack and defense may differ from those used in real fighting (Pellis 1988; 1993), and since a motor skill can only be practiced effectively if the *exact* same motor pattern is undertaken (Stamps 1995; Byers 1998), play fighting cannot assist in the refinement of fighting skills. Pellis & Pellis (1998) also showed that the most challenging aspects of real fighting (e.g. blocking an attack) are frequently absent from play fighting, making play a poor candidate for the rehearsal of combat skills.

A number of experimental studies have also failed to detect any evidence of play providing practice. Thomas and Schaller (1954) found that kittens reared without play (through social isolation and the wearing of translucent goggles that prevented object play) did not differ in their prey-catching behaviour from kittens reared normally. Similarly, Caro (1980) showed that kittens denied the opportunity to undertake object play did not differ (for 25 different measures of predatory skill) from kittens raised in a toy-enriched environment. Davies and Kemble (1983), documenting individual variation in the play of northern grasshopper mice, *Onychomys leucogaster*, found no correlation between any measure of play and subsequent predatory ability; and nor did Vincent and Bekoff (1978) who undertook a similar study with young coyotes. Chalmers and Locke-Haydon (1984) compared the frequency of social play of individual common marmosets with the individual's ability to perform a large range of sensorimotor and social skills. They concluded: "a major feature of our results is the absence of correlations".

The only positive experimental evidence in support of the practice hypothesis comes from social deprivation studies. Male rats reared in isolation exhibit subsequent incompetence in sexual performance (Hard & Larsson 1971), having difficulty achieving the appropriate orientation when mounting. Rearing juvenile rats with non-playful (drugged) partners does not rectify the problem (Einon et al. 1978), suggesting that orientating skills are perfected during social play rather than through simple social contact. However, Pellis and Pellis

(1998) argue that play fighting in rats does not include the evasive manoeuvres normally exhibited by the female rat during mating, making play an inadequate means of practicing mating skills for males.

1.3.4 Energy regulation

These hypotheses suggest that play is designed to promote adaptive energy loss (Spencer 1898). The energy regulation hypotheses propose that play:

- expends 'surplus' energy, allowing individuals to increase food consumption (to maximize protein intake for growth) without incurring the costs of obesity (Burghardt 1988; Barber 1991);
- activates the sympathetic nervous system which increases heat production in brown adipose tissue, increasing an individual's resistance to both pathogens and cold exposure (Barber 1991).

The strongest support for the 'surplus' energy hypothesis is provided by the finding that frequency of play appears to be positively related to food consumption in a variety of species (Southwick 1967; Loy 1970; Baldwin & Baldwin 1974; Lee 1984; Barrett et al. 1992; Sommer & Mendoza-Granados 1995; Nunes et al. 1999) as specifically predicted by Barber (1991). However, contrasting results were obtained in a series of laboratory experiments with domestic kittens (Bateson et al. 1990) and infant rats (Smith 1991; Loranca et al. 1999), in which conditions normally associated with food deprivation actually increased subsequent rates of play. There is also good experimental evidence to suggest that the increases in rate of play often observed during periods of increased food availability are caused by alterations to time budgets rather than by energetic factors per se (i.e. foraging time is reduced so more time is available for play). Baldwin & Baldwin (1976) made the food of captive squirrel monkeys time-consuming to obtain (by requiring them to extract powdered food from a container) and the monkeys played at only one percent of their normal level. Similarly, Muller-Schwarze et al. (1982) reduced the milk provided to white-tailed deer fawns, and although the fawns fully compensated energetically for the reduction in milk by increasing the time they spent grazing, their rate of play fell by 35%.

The fact that juvenile animals exhibit the highest rates of play (Fagen 1981, Smith 1982) is consistent with the 'surplus' energy hypothesis, since animals of this age not only need to maximize growth, but, in many species, they suffer elevated predation rates (e.g. Dunbar

1980; Gosling 1986; Jarman & Southwell 1986; Moehlmann 1986; Rood 1986; Clutton-Brock et al. 1999a), and can thus least afford to carry the costs of obesity (Berg 1960; Pond 1981; Rothwell & Stock 1981), such as increased vulnerability to predators. However, it appears that play is not particularly effective in preventing obesity in young mammals. Nunes et al. (1999) found that provisioned Belding's ground squirrels became significantly fatter than controls, despite increasing their rate of play, and Renouf (1993) showed that rates of play in captive harbour seals (*Phoca vitulina*) were at their highest during seasonal fat accumulation!

There is currently little evidence to support or refute the thermogenesis hypothesis of play, although the physical characteristics of play (vigorous, three-dimensional movement that stimulates the vestibular system, and motor patterns derived from 'high arousal' emergency situations) make it well suited for the activation of the sympathetic nervous system (Barber 1991). While the overall phylogenetic and ontogenetic distribution of play behaviour is similar to that of brown adipose tissue (i.e. common in mammals, rare in birds, apparently nonexistent in reptiles; and most prevalent in immature animals – Barber 1991), there is nothing to suggest that mammal species that retain brown adipose tissue into adulthood (e.g. hibernators) show more adult play, and the hypothesis cannot account for the presence of adult play in many species that do not retain brown adipose tissue. While no attempt has been made to test the effect of play on immunocompetance or thermoregulation, frequency of play in ponies (*Equus callabus*) is inversely related to ambient temperature (Crowell-Davis et al. 1987), which is consistent with the hypothesis that play is used to combat exposure to the cold.

1.3.5 Other physiological benefits

These hypotheses suggest that play provides individuals with a diverse array of physiological benefits. The physiological hypotheses propose that play:

- provides exercise to increase an individual's physical fitness, i.e. cardio-vascular capacity, endurance and skeleto-muscular strength (Brownlee 1954; Fagen 1976, 1981; Bekoff 1988, 1989; Gomendio 1988; Hass & Jenni 1993);
- exercises muscles that are normally used only in adulthood (e.g. in fighting or mating) to prevent their atrophy (Brownlee 1954);
- modifies synapse distribution in the cerebellum (Byers & Walker 1995; Byers 1998);

- ensures the appropriate differentiation of muscle fibre type (Byers & Walker 1995; Byers 1998);
- makes individuals feel happy and relaxed, thereby increasing their overall health and fitness (McGhee 1979; Lewis 1982).

While play evidently does provide young mammals with 'exercise', it is clear from the burgeoning literature on sports physiology that it is unlikely to be effective in raising an animal's physical fitness. The benefits of exercise training (increased endurance and strength) can only be acquired if a subject exercises continuously until near-fatigue (Scheuer & Tipton 1977; Nieman 1990; Byers & Walker 1995). Such sustained bouts of exercise rarely, if ever, occur during play; in fact, the average duration of play bouts in numerous species is only 5 to 20 seconds (e.g. Owens 1975a; Dane 1977; Symons 1978b; Hole 1988; Thompson 1985; Fry 1987; Watson & Croft 1993). As an example, play bouts in Norway rats generally last 5 to 8 seconds (Birke & Sadler 1983), but exercise bouts of one hour are needed to produce an exercise training response in this species (Xia 1990). Another important characteristic of 'physical fitness' is that its benefits are transitory, and they rapidly diminish once exercise ceases (Nieman 1990; Byers & Walker 1995). This casts serious doubt on the hypothesis that play serves to maintain muscles needed only in adulthood (Brownlee 1954), since play, in the majority of species, ceases, or drops to very low levels, many months prior to the appearance of serious mating or fighting behaviour.

While it is known that motor activity during early postnatal development can affect cerebellar synapse formation (Floeter & Greenough 1979; Pysh & Weiss 1979; Brown et al. 1991), the only evidence to suggest that play functions to modify synapse distribution, is a rough correlation - in the three species for which data is available (laboratory rat, house mouse and domestic cat) - between the age at which play is most frequent and the terminal phases of cerebellar synaptogenesis (Byers & Walker 1995). However, at least 80% of cerebellar synapses are already complete prior to the appearance of play (Byers & Walker 1995) and, in many species, play persists well beyond the 'sensitive period' for synaptogenesis. There is no evidence to support the hypothesis that play facilitates the development of appropriate muscle fibre types (i.e. the ratio of slow to fast fibres in a muscle). In vitro studies suggest that muscle fibre type is fixed early in neonatal development (Bandman et al. 1982; Miller & Stockdale 1986; Schafer et al. 1987) and, if postnatal changes are possible, they are determined by the pattern of innervation in the muscle (Buller et al.

1960; Armstrong 1980; Baldwin 1984); however, neither rats nor mice undertake play during the period when muscle fibre innervation is fixed (Byers & Walker 1995).

The hypothesis that play enhances an individual's health by providing interludes of relaxation and 'fun' has received little recognition, even though it is well established that emotional state can influence human health, longevity and productivity (e.g. Cherry 1980; Lewis & Michalson 1982), and that unremitting stress severely impairs immunocompetance (Lee & Cockburn 1985; Sapolsky 1993; Apanius 1998). While the physiological consequences of play remain unclear, play behaviour is known to be associated with elevated levels of endogenous opioids (Panskepp et al. 1985; Vanderschuren et al. 1995; Siviy 1998), and mammals find it both rewarding and pleasurable (Humphreys & Einon 1981; Normansell & Panskepp 1990; Calcagnetti & Schechter 1992; Pellis & McKenna 1995). However, it is appears that individuals suffering high levels of stress reduce play (Hetherington et. al. 1979; Hutt 1979b; Fagen 1981; Suomi 1982; Biben 1998), which is contrary to the expectations of the hypothesis. This hypothesis also fails to account for age and gender differences observed in play (since all animals should benefit equally from playing), but play's age/sex distribution could be caused by unequally distributed costs and constraints, rather than benefits (e.g. the high cost of reproduction for female mammals may place an energetic constraint upon play in this sex).

1.3.6 Cognitive development

The cognitive hypotheses suggest that play:

- teaches individuals how to cope with unexpected events that cause stress and sudden loss of control (Spinka et al. 2001);
- provides individuals with immediate feedback about their own physical abilities, allowing them to accurately evaluate physical or social risks (Thompson 1996, 1998);
- provides experience of both winning and losing in a non-threatening context, thereby increasing an animal's confidence and reducing the stress associated with the risks of bodily contact (Biben 1998);
- encourages individuals to learn that they have the capacity to control their own behaviour (Piaget 1962; Fein 1982; Schwartzman 1982);
- increases behavioural flexibility (Bruner 1972; Fagen 1981, 1982; Eibl-Eibesfeldt 1982), innovation (Fedigan 1972; Vandenberg 1978, 1981, 1982) and problem-

solving ability (Piaget 1962; Sutton-Smith 1967; Smith & Dutton 1979; Smith & Smith 1984);

- enhances intelligence and learning ability (Piaget 1962; Hutt 1979a, 1979b; Ferchmin & Eterovic 1979, 1982; Fein 1982; Suomi 1982).

The difficulty of quantifying cognitive development, particularly in non-human animals, is a major impediment to the assessment of the cognitive hypotheses. While some relevant findings are available from studies of children, such data needs to be treated cautiously, since many components of human play (e.g. fantasy, linguistic and sociodramatic play) seem to be unique to our species (Martin & Caro 1985). However, as noted by Suomi (1982), there is good indirect evidence that play is involved in cerebral development. Firstly, play is virtually non-existent in animals without a cerebral cortex, secondly, there is a positive correlation between prevalence of play and relative brain mass, when taxa are compared (e.g. Ortega & Bekoff 1987; Byers 1999), and thirdly, ontogenetic peaks in play coincide closely with periods of maximum cortical growth and differentiation.

More direct evidence is provided by laboratory studies that have shown that young rodents exposed to a complex environment (social and physical) develop heavier cerebral cortices (Rosenzweig & Bennett 1978), greater neural connectivity (Ferchmin et al.1970; Volkmar & Greenough 1972; Rosenzweig et al. 1978; Juraska et al. 1980) and better learning abilities (Rosenzweig & Bennett 1977) than littermates raised in impoverished environments. An evaluation of the components of environmental enrichment (Ferchmin et al. 1975, 1980; Ferchmin & Eterovic 1977, 1978) has established that sensory stimulation, plus arousal, are able to increase cortical growth only if they are accompanied by interactive behaviour (i.e. play or training), with play behaviour showing the strongest effect (Rosenzweig et al. 1968; Bennett et al. 1979; Ferchmin et al. 1980; Ferchmin & Eterovic 1982). The speed with which cortex weight increases is also positively related to frequency of play (Ferchmin & Eterovic 1982), with weanling rats (that play more vigorously than other age classes) developing heavier cortices in only four days (Rosenzweig et al. 1978). Environmental complexity appears to have a similar effect in primates (Gluck et al. 1973; Floeter & Greenough 1979), and is known to improve mental development in disadvantaged children (Hunt 1976).

Neurological studies designed to identify which areas of the brain are critical to play, have revealed that, unlike most behaviours, play leads to the widespread activation of the whole cortex, plus a number of subcortical structures, such as the thalamus and hippocampus (Siviy

1998). This global activation of the brain should greatly facilitate learning (since learning is activity-dependent - Kaczmarek 1993), and also encourage the formation of neural connections between brain areas that are normally not connected, potentially enhancing creativity and innovation (Siviy 1998). Rats deprived of play (through social isolation or the drugging of companions), during the period in which play is most frequent, are slower than normal rats to learn new information, such as habituating to novel stimuli, or reversing learned discriminations (Einon et al. 1978).

It has also been established that a range of different neurochemical systems are involved in play, including the monoamines, dopamine, norepinephrine and serotonin (Siviy 1998). These monoamines also coordinate an animal's response to stress (Goldstein et al. 1996), and a behaviour that activates them globally, such as play, will almost certainly alter the future sensitivity of these monaminergic systems (e.g. Antelman et al. 1992). In this way play experience may improve the brain's ability to handle psychological stressors (Siviy 1998), as proposed by two of the cognitive hypotheses (Biben 1998; Spinka et al. 2001). Consistent with these predictions is the finding that rats isolated during the period when play is most frequent are unable to deal appropriately with social stressors (showing hypo- or hyper-defensiveness toward conspecifics – Potegal and Einon 1989; Hol et al. 1994, 1999; van den Berg et al. 1999), and have higher plasma corticosterone and epinephrine concentrations than normal rats (van den Berg et al. 1999). However, these differences can be eliminated by providing isolates with one hour of play experience daily (Potegal and Einon 1989). There also appears to be a positive correlation, in humans, between childhood play experience and the ability to cope with stressful life experiences (Brown 1998; Saunders et al. 1999).

This evidence that play influences stress responses supports the 'training for the unexpected' hypothesis (Spinka et al. 2001), which asserts that play helps an animal develop flexible kinematic and emotional responses to unexpected events that involve loss of control and stress. This hypothesis also offers an explanation for the high frequency of play observed in juvenile mammals (animals undergoing rapid allometric growth must play more frequently to learn how to handle their changing body proportions), and the tendency for play to be stimulated by novel objects and environments (Wood-Gush & Vestergaard 1991; Jensen et al. 1998), as animals must learn how to cope with unfamiliar things. However, integral to this hypothesis is the tenet that self-handicapping is a fundamental characteristic of play, since playing individuals must create situations in which they temporarily lose control. However, there is good evidence that individuals go to considerable lengths to *avoid* 'losing control' during play. In many species (e.g. Owens 1975b; Byers 1980; Boulton 1991; Biben 1989,

1998) individuals eschew adopting the losing role while play fighting, preferentially initiating play with partners that they can defeat, and avoiding those that are likely to defeat them. Biben (1989) found that in dyads of squirrel monkeys, frequency of play was considerably reduced if one partner lost more than 60% of the time, and she demonstrated experimentally that individuals that were unlikely to win play wrestling bouts avoided 'directional' wrestling (in which one individual gained control of the other by pinning it down) and instead favoured 'non-directional' wrestling, in which there could be no clear winner (e.g. play fighting while hanging from a limb). The strong preference that many taxa show for play partners closely matched in size (e.g. Breuggeman 1978; Berger 1980; Byers 1980; Stevenson & Poole 1982; Boulton 1991; Watson 1993; Thompson 1996) is also consistent with the argument that individuals are trying to maximize their likelihood of winning. Several researchers (Sutton-Smith 1993, 1995; Biben 1998) have even suggested that the psychological empowerment generated by winning is an important benefit of play, and a study of children found that repeated losing in play can have negative social and psychological consequences (Sutton-Smith & Kelly-Byrne 1984).

Spinka et al. (2001) argue convincingly that play signals, used for the initiation and continuation of play, are derived from self-handicapping gestures (e.g. rolling over, pivoting, running backwards) that are diametrically opposed to the postures adopted in threat displays (the canid 'play bow', for example, which lowers the front half of the body, is the antithesis of the canid 'standing-tall' threat stance – Bekoff 1977c). Spinka et al. claim that such signals evolved because self-handicapping behaviours are an intrinsic and essential characteristic of play (so players can gain practice at coping with awkward situations), but these signals (which place an animal in a compromised position) also give the message: "You can defeat me!", which is supportive of the argument that winning is of greater value to a playing individual than gaining experiencing at losing.

The issue of self-handicapping is also of central importance to the 'self-assessment' hypothesis of play (Thompson 1998), since animals cannot accurately compare their physical abilities with those of others if their playmates are not exerting their full capacity. While self-handicapping is known to sometimes occur during play (e.g. Mendoza-Granados & Sommer 1995; Watson & Croft 1996; Biben 1998; Pereira & Preisser 1998), it is generally only observed when an absence of well-matched partners necessitates play between mismatched individuals (Biben 1998) e.g. adults playing with their offspring. A number of studies have compared win-lose asymmetries in play fights with those seen in concurrent aggressive interactions. No correlation was detected for domestic horses, (Araba & Crowell-Davis

1994), red-necked wallabies (Watson 1993), rhesus monkeys (Symons 1978a) or female baboons (Owens 1975b), but a positive relationship was found for squirrel monkeys (Biben 1998) and male baboons (Owens 1975b). However, in almost all species studied, win-lose asymmetries are less pronounced in play than in aggression. Thompson (1998) suggests that this greater ambiguity in relationships during play, rather than being indicative of self-handicapping in play, is an accurate reflection of differences in competitive ability (which are likely to be subtle), whereas the highly polarized interactions seen during aggression are caused by subordinates trying to avoid confrontation with dominant individuals (Bernstein 1981).

The hypothesis that play functions to increase behavioural flexibility, innovation and problem-solving ability has been the subject of numerous human studies (Dansky & Silverman 1973, 1975; Sylva et al. 1976; Sylva 1977; Smith & Dutton 1979; Pepler & Ross 1981; Smith et al. 1981; Vandenberg 1981; Cheyne & Rubin 1983; Christie 1983; Smith & Simon 1984), yet results remain ambiguous. Many animal studies (e.g. Birch 1945; Epstein et al. 1984) have found that individuals are better able to solve a problem, or perform a task, if they have had prior experience with the elements involved in the task (such as that provided by play). In primate taxa, object manipulation during play appears to co-vary with tool use (Smith 1982) – for example, young chimpanzees regularly include leaf-sponging or twig-poking behaviours in their play (McGrew 1977) - suggesting that play may facilitate the learning of such skills. However, human studies have found that, whereas prior play seems to alter the way children approach or think through a problem, generally increasing their ability to make unusual associations (Danksy & Silverman 1973, 1975; Sylva et al. 1976; Sylva 1977; Cheyne 1982), this led to no greater improvement in ability to solve the problem than did other forms of prior experience, such as observation or imitation (Vandenberg 1981; Cheyne 1982; Christie 1983; Simon & Smith 1983; Smith & Simon 1984). In fact, a number of studies found that play actually impeded problem solving (e.g. Schiller 1957; Hutt 1966) because it acted as a distraction.

1.4 AIMS OF THIS STUDY

As can be seen from Section 1.3, there is currently little concrete evidence available to support any of the hypotheses advanced to explain the adaptive significance of play. The belief, widespread in the 1970s and early 80s, that detailed quantification of play behaviour in a variety of taxa would ultimately reveal the function of play, was erroneous, and, since that time, few attempts have been made to devise testable predictions or to conduct hypothesis-testing studies of play.

Clearly, it is not possible for a single study to evaluate all of the hypotheses of function, and this study sets out to test those that are of particular relevance to social species. Using data from a wild population of meerkats (*Suricata suricatta*), the study evaluates four hypotheses relating to social bonding: (1) that play reduces aggression between playmates; (2) that play enhances group cohesion, thus increasing an individual's fidelity to its group; (3) that play strengthens alliances between individuals, enhancing future cooperation; and (4) that play helps to establish and maintain dominance hierarchies, without aggression. The study also evaluates the practice hypothesis for play fighting, tests some of the predictions arising from the self-assessment hypothesis and addresses the question of whether play carries an energetic cost, by assessing experimentally the relationship between play and nutrition.

1.5 STUDY SPECIES

1.5.1 Phylogeny and distribution

The meerkat, or suricate (*Suricata suricatta,* Schreber 1776), is a small (700g), diurnal mongoose belonging to the family Herpestidae (Veron et al. 2003) within the order Carnivora (although some authors place the group, as a subfamily, within the family Viverridae - Skinner & Smithers 1990). The Herpestidae includes all extant mongoose species - 37 species in 18 genera – and its members are found primarily in Africa with 8 species in Asia (Veron et al. 2003). The fossil record suggests that the first true herpestid appeared in Africa in the early Miocene (17.8 million years ago), having evolved from feliforms known to be present approximately 2 million years earlier (Hunt 1996). The genus *Suricata* is considered to belong to the subfamily of social mongooses (the Mungotinae; Wozencraft 1989) although it is taxonomically distinct from the other members of this group, due to morphological specialization to its dry, open habitat (Veron et al. 2003). *Suricata* is represented by a single species, although three subspecies are recognized: *S. s. suricatta* (the subject of this study), *S. s. marjoriae* and *S. s. iona* (Skinner & Smithers 1990).

Meerkats are confined to southern Africa (including South Africa, Namibia, Botswana and Angola) where they are locally common in the South-West Arid Zone and adjacent Southern Savanna, Karoo and Highveld regions (Skinner & Smithers 1990; Estes 1991).

1.5.2 Social organization

Although the majority of Herpestid mongooses are solitary, ten species are known to live in groups or clans (Rood 1986; Estes 1991), and three of these - the banded mongoose, *Mungos mungo* (Cant 2000), the meerkat (Clutton-Brock et al. 2001a), and the dwarf mongoose, *Helogale parvula* (Rood 1990) - are obligate social species.

Meerkats live in groups of 3-40 individuals, and group size is positively related to individual survival, growth rate and female fecundity (Clutton-Brock et al.1999a, 2001b, 2001c; Russell et al. 2002, 2003a) and group survival (Clutton-Brock et al. 1999a, 1999b; Courchamp et al. 1999). Groups are normally comprised of a dominant breeding pair (responsible for 75% of the group's pups), the pair's grown offspring and several immigrant males (Clutton-Brock et al. 2001b). Meerkats are obligate cooperative breeders (Clutton-Brock et al. 2001a) and all group members make substantial contributions to group activities, such as the raising of pups (Doolan & MacDonald 1997a, 1999; Clutton-Brock et al. 1998b, 2000, 2001a, 2001c, 2002; Brotherton et al. 2000; Russell et al. 2002, 2003a, 2003b) and anti-predator behaviour (Manser 1999; Clutton-Brock et al. 1999c).

Breeding success in meerkats is strongly correlated with rainfall (Clutton-Brock et al. 1999b), and, in good years, meerkat groups can raise four litters of 1-7 pups (mean 4.1) annually (Clutton Brock et al. 1999a). The pups first emerge from their natal burrow at around 3 weeks of age, and begin travelling with the group at 4 weeks of age. (Doolan & MacDonald 1999). They are dependent upon provisioning by group members until they are around 3 months old (Brotherton et al. 2001). They attain sexual maturity at 7-11 months of age, and disperse from their natal group, with same-sexed group members, at 18-30 months of age (Clutton-Brock et al. 1998a). Females are aggressively expelled from their natal group by the group's dominant female when she is in the latter stages of pregnancy, and females often suffer several short-term evictions (across a number of the dominant's breeding attempts) before finally emigrating from the group (Clutton-Brock et al. 1998a). In contrast, males disperse voluntarily after undertaking repeated short-term prospecting forays to neighbouring groups, to solicit matings with foreign females and assess the potential for taking over, or joining, the group (Doolan & MacDonald 1996b, Young 2003). Dispersing meerkats set up new groups with opposite-sexed dispersers from other groups, or (in the case of males) join, or seize dominance in, established groups (Doolan & MacDonald 1996b; Clutton-Brock et al. 1998a).

1.5.3 Ecology

Meerkats, which are terrestrial and diurnal, live in a drier and more open habitat than any other species of mongoose (Estes 1991). They possess territories of approximately 1-2 km^2, which they defend from neighbouring groups using scent marking (Gsell 2002), visual displays (Ewer 1963) and, if necessary, fighting (Doolan & MacDonald 1996b). Meerkat territories encompass a number of extensive burrow systems (often shared with ground squirrels, *Xerus inauris*, and yellow mongooses, *Cynictis penicillata*), to which the group retires at night or in the event of rain (Skinner & Smithers 1990; Doolan & Macdonald 1996a). Groups normally emerge from the burrow at sunrise each day and group members remain around the burrow mouth for up to 2 hours, sunning, grooming and playing, before setting off to forage. Although meerkats forage as a group (individually digging up arthropods and small vertebrates), they never cooperate to catch prey (Doolan & Macdonald 1996a). During the hotter months of the year, they suspend foraging after 3-4 hours, to rest in the shade or down a burrow until late afternoon, but in winter they forage continuously throughout the day. Since meerkats are particularly vulnerable to attack by predators when digging for prey, groups post a sentinel when they are foraging (Clutton-Brock et al. 1999b; Manser 1999). They also maintain several thousand bolt-holes (for predator-escape) across their home range (Manser in press) and employ a sophisticated system of alarm vocalizations (Manser 2001; Manser et al. 2001, 2002). However, predation levels are still high (Clutton-Brock et al. 1999a), primarily due to aerial predators.

1.5.4 Play

Play occurs in the young of all known herpestid species (Estes 1991), but studies of play within this group are limited to descriptions of play in captive individuals for three species: ichneumons, *Herpestes ichneumon* (Rensch & Ducker 1959), dwarf mongooses (Rasa 1984) and meerkats (Ewer 1963; Wemmer and Flemming 1974). Although studies of play in wild populations are a rarity for almost all taxonomic groups, only one field study has examined play behaviour in a terrestrial carnivore (cheetah cubs in the Serengeti – Caro 1987, 1995).

Meerkat play, which is undertaken by all group members (Estes 1991), consists primarily of social play, or play fighting (Ewer 1963). Wemmer and Fleming (1974) produced a detailed quantitative description of play in a captive family of six meerkats (one adult male and female, and their four offspring) when the youngsters were aged from 1-6 months. They identified the following behavioural components of meerkat social play:

Pawing – A foreleg was extended toward, and sometimes touched, a companion's body.

Clasping – A part of a companion's body was grasped with the forelimbs. This movement occurred frequently during grappling, wrestling and mounting.

Standing-on – One animal supported its forelegs on top of the torso of a quadrapedally standing or sitting companion.

Biting – Inhibited bites were applied to any part of the companion's body. Bite targets varied with body orientation, but approximately half of all bites were directed at the head or neck, and one-third at the trunk. Bite targets did not change with age, but biting (and forelimb contact) was less frequent when animals were aged 3-6 months than when 1-3-months old.

Grappling – Both animals stood bipedally and clasped each other around the neck, shoulders or chest with their forelimbs. Both animals leaned and pushed against the other while attempting to bite their opponent's head or neck. Grappling was mainly restricted to play interactions between animals of similar size.

Wrestling - One animal lay on its side or back while its companion stood over it, with its forefeet on the animal's ventrum or side, or on the substrate.

Mounting - One animal supported its fore body upon its companion's back while clasping the other's sides, between the ribcage and groin. Mount duration varied from less than a second to more than a minute.

Side-pressing – The animal leaned against its companion with its neck, shoulder or side while standing in place or slowly walking forward.

Stiff-legged rocking gait – An exaggerated bounding gallop in which the back was strongly arched. It was sometimes performed with no forward progression (i.e. the animal remained in the same place), and could be accompanied by exuberant rotational movements of the head and neck.

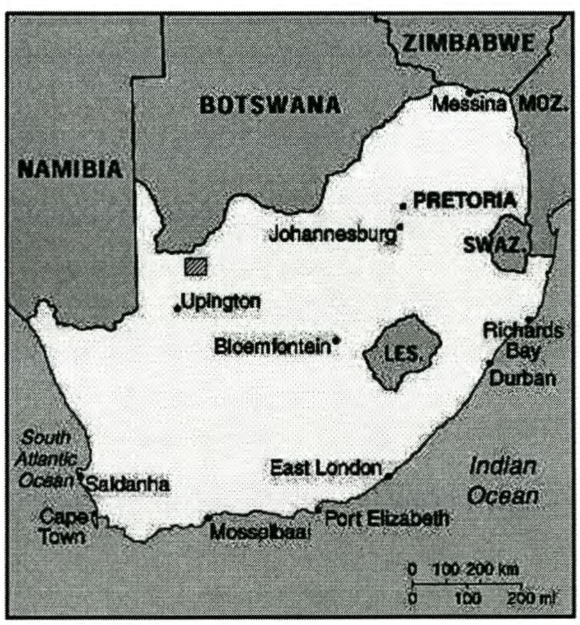
Wemmer & Flemming (1974) found that the frequency of play in their family of meerkats oscillated greatly from week to week, and that the father played with the litter of youngsters more frequently than did the mother. They also found no evidence of unequivocal play-soliciting behaviour patterns. However, as in dwarf mongooses (Rasa 1984), wild meerkats do emit a distinctive 'play' vocalization (the 'excitement call' – Manser 1998), but it is not known whether this call is reserved exclusively for play.

1.6 STUDY SITE

1.6.1 Location

The fieldwork for this study was carried out in the southern Kalahari Desert, 30 km west of Van Zylsrus, South Africa (26°50' S, 22°30' E; Fig. 1.1) at a research site established, in 1993, by researchers from the University of Cambridge. The site encompassed approximately 5,000 hectares of uncultivated ranchland (at an average altitude of 900m), including part of the Kalahari Research Trust's Kuruman River Reserve.

Figure 1.1. Location of the study site (hatched box) in South Africa.



1.6.2 Habitat

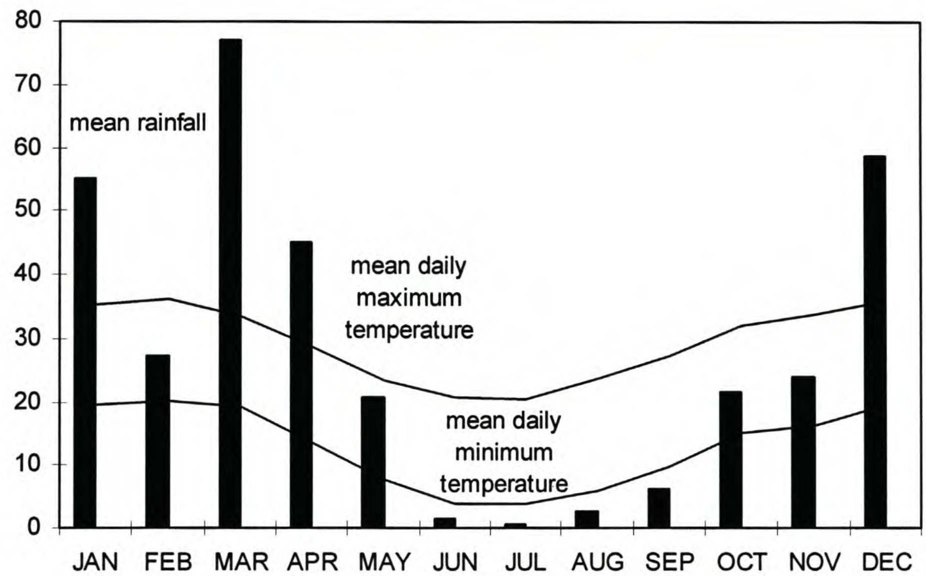
The vegetation at the study site was typical Kalahari thornveld (Cowling et al. 1997). It was comprised of three distinct zones: the dry bed of the Kuruman River, the adjacent river terraces, and extensive areas of low (10-30m), lightly vegetated sand dunes. The riverbed was mostly non-vegetated apart from dense thickets of mesquite, *Prosopis glandulosa*, an exotic species introduced from North America (Palgrave 1988). The banks of the river were lined with large camel thorn trees, *Acacia erioloba,* that also grew, more sparsely, on the river terraces and in the swales between the dunes. However, the river terraces were primarily dominated by low shrubs, such as driedoring, *Rhigozum trichotomum*, perdebos, *Monechma foliosum,* and blue bush, *Monechma incanum*. Perennial grasses (*Eragrostis* spp., *Aristida* spp., *Stipagrostis* spp., *Schmidtia* spp.,) also occurred on the terraces, and dominated on the dunes, proliferating after rain, along with many small annuals, such as the devil's thorn, *Tribulus* spp., and vlei lily, *Nerine laticome*. Other common and widespread species were the black thorn, *Acacia mellifera*, grey camel thorn, *Acacia haemotoxylon*, shepherd's tree, *Boscia albitrunca*, velvet raisin bush, *Grewia flava,* and hook thorn, *Ziziphus* spp.

The study site was grazed by both domestic livestock (goats, sheep, cattle, horses) and native species – steenbok, *Raphicerus campestris*, gray duiker, *Sylicapra grimmia*, springbok, *Antidorcas marsupialis*, gemsbok, *Oryx gazella*, red hartebeest, *Alcelaphus buselaphus*, and ostrich, *Struthio camelus*. Although no large carnivores survived in the area (having been eradicated about 60 years previously), many smaller predators (capable of predating meerkats) were still present, including the black-backed jackal, *Canis mesomelas*, caracal, *Felis caracal*, African wildcat, *Felis libyca*, slender mongoose, *Herpestes sanguineus*, yellow mongoose, rock monitor, *Varanus exanthematicus*, cape cobra, *Naja nivea,* and puff adder, *Bitis arietans*. Domestic dogs and cats were also present. Raptor densities were also probably reduced due to persecution by farmers, but tawny, *Aquila rapax*, martial, *Polemaetus bellicosus,* and black-chested snake, *Circaetus pectoralis,* eagles, and southern pale chanting goshawks, *Melierax canorus,* were sighted frequently.

1.6.3 Climate

The Kalahari is located in the latitudinal zone of semi-permanent high pressure (produced by descending air from the inter-tropical convergence zone), resulting in a low and erratic rainfall regime (Mills & Haagner 1989). Mean annual precipitation at the study site was 250 mm, but annual totals during the main period of data collection (1997-2002) averaged 306 mm, with a range of 200-503 mm (rainfall was measured at the site using a standard rain gauge). Precipitation was mainly restricted to the hotter months (October to March; Fig. 1.2). Temperatures at the site were extreme (daily maximum and minimum air temperatures were measured using an alcohol thermometer suspended in the shade), often rising above 40°C during summer and dropping below freezing on winter nights (Fig. 1.2).

Figure 1.2. Mean monthly rainfall (mm), and daily maximum and minimum temperatures (°Celsius) at the study site, 1997-2002.



1.6.4 Study population

During the course of this study, more than 550 individual meerkats from 11 groups contributed to the data. Almost all these animals were well habituated to the presence of researchers (most having been born into habituated groups), and thus it was possible to make close behavioural observations (within 1 metre) and, where necessary, handle individual animals (e.g. for weighing or marking).

Each meerkat group was visited several times per week (one group member wore a radio-transmitter collar), and detailed life history records were maintained for all individual group members. When a female was in the latter stages of pregnancy, her group was visited on a daily basis, and thus exact birth dates were known for almost all individuals in the study population. Once a litter of pups had emerged from its natal burrow, each pup was given a unique name code and fitted with a transponder chip (inserted subcutaneously at the back of the neck) to provide permanent identification. A skin sample was also taken from the pup's tail tip (to determine parentage and degree of relatedness through microsatellite genetic analysis - Griffin et al. 2003), and the animal was marked with a small patch of trimmed or dyed fur (using black, human hair dye). These identifying marks were maintained throughout the animal's life, by reapplying them every few weeks while the animal was sunning at the burrow. For the collection of play data, additional coloured marks were applied to each animal's tail (using permanent marker pen) so that individuals could be rapidly identified even when partially obscured during social play.

CHAPTER TWO

EXPERIMENTAL PROVISIONING INCREASES PLAY IN FREE-RANGING MEERKATS

(*Animal Behaviour*, 2002, 64, 113-121)

2.1 ABSTRACT

The sensitivity of play to variations in food availability has been cited as evidence of the costliness of play, since energetically stressed animals dispense with costly behaviours. However, the causality of the relationship between nutrition and play has not been adequately tested. Using weight gain as a measure of food intake, I documented the food consumption of free-ranging meerkat pups, *Suricata suricatta,* and found that long-term nutritional status (weight gain over a 6-week period) was positively correlated with rates of play. The causality of this relationship was confirmed by conducting long-term (4-8 weeks) provisioning experiments that raised the nutritional status of experimental pups, subadults and adults. Experimental animals more than doubled their rate of play compared to their non-provisioned controls. Short-term variations in food consumption (daily weight gain) were not correlated with subsequent rates of play, and I used a short-term feeding experiment to document the transitory effects of hunger satiation. The study established that an increase in available energy contributed to the increase in rates of play, rather than the animals simply having more time available to play as a result of being released from the constraints of foraging. I conclude that play in meerkats was energetically costly, and must be adaptive given that the cost of play to juvenile meerkats (in terms of future reproductive success) was potentially high.

2.2 INTRODUCTION

Despite several decades of study, and postulation of more than 30 hypotheses (Smith 1982; Baldwin 1986), the adaptive significance of play remains uncertain (Caro 1988; Spinka et al. 2001). The failure to identify a single, all-encompassing function of play has been ascribed variously to the difficulty of detecting benefits that are delayed (Martin & Caro 1985) or physiological (Byers & Walker 1995), the possibility that play is simply a by-product of juvenile development which has been co-opted for different purposes by different species (Coppinger & Smith 1989), or that play provides an organism with minimal benefits but is retained because it is not costly (Martin & Caro 1985). To test the last of these hypotheses, a number of studies have attempted to quantify the cost of play (Martin 1984b; Miller & Byers 1991; Siviy & Atrens 1992) but have been faced with the inevitable question of how much is costly (Bekoff & Byers 1992). However, the fact that play is so labile may provide evidence of its inherent costliness (Martin & Caro 1985).

Play has traditionally been viewed as a highly variable behaviour, with rates of play fluctuating in response to prevailing conditions, particularly the availability of food (Fagen 1981; Martin & Caro 1985; Barber 1991). Responsiveness to nutritional state would be evidence that play is costly, since an energetically stressed organism should forgo those behaviours that cost most; however, the assumption that rates of play fluctuate with nutrition has not been adequately tested. Despite evidence that primates curtail play when facing starvation (Southwick 1967; Loy 1970; Baldwin & Baldwin 1974) there is only limited evidence that play responds to fluctuations in nutrition under nonlife-threatening conditions. Although Lee (1984) found a positive correlation between quality of diet and rate of play in vervet monkeys, *Cercopithecus aethiops,* when comparing wet and dry seasons, and a similar relationship has been detected between habitat quality and play in mountain sheep lambs, *Ovis canadensis* (Geist 1971), gelada baboons, *Theropithecus gelada* (Barrett et al. 1992), and Hanuman langurs, *Presbytis entellus* (Sommer & Mendoza-Granados 1995), the causality of these relationships was never established. Only one experimental study has demonstrated a causal link between plane of nutrition and play: Nunes et al. (1999) found that provisioning significantly increased rates of play in juvenile Belding's ground squirrels, *Spermophilus beldingi.* However, because sciurid populations are generally not limited by food (during their active seasons), and the provisioned squirrels spent less time foraging, Nunes et al. concluded that it was the trade off between time devoted to feeding and play that limited play behaviour under non-experimental conditions. This is consistent with the findings of studies by Muller-Schwarze et al. (1982) and Baldwin & Baldwin (1976) who showed that a decrease in the accessibility of food (and consequent increase in the time spent foraging) rather than energetic factors, caused a reduction in play (see Section 2.5 for further details). In contrast to these findings, a series of laboratory experiments with domestic kittens, *Felis cattus* (Bateson et al. 1990) found that conditions normally associated with food deprivation increased their subsequent rate of play. Infant rats, *Rattus norvegicus*, also behave in this way (Smith 1991; Loranca et al. 1999).

This study examines the relationship between nutrition and play in a population of wild meerkats, *Suricata suricatta,* in the southern Kalahari. Initially I investigated whether there is a relationship between natural variation in food consumption and rate of play, under favourable (nonfood-stressed) conditions. I then used a series of provisioning experiments to test the causality of the relationship between food and play, and to establish whether changes in time budgets alone, rather than energetic factors, are responsible.

2.3 METHODS

2.3.1 Study population

I undertook the study between August 1997 and October 2000, collecting data from eight groups of free-ranging meerkats living on ranchland in the southern Kalahari, 30 km west of Van Zylsrus, South Africa (26°58'S, 21°49'E). See Section 1.6 for details of the study site's topography, vegetation and rainfall. The study was carried out under a permit issued by the Northern Cape Conservation Service, South Africa.

Meerkats are desert-adapted, cooperative mongooses that live in groups of 3-40 individuals. When conditions are favourable, a meerkat group can raise four litters of pups annually, with emergent litter size averaging four pups (Clutton-Brock et al. 1999a). The pups spend their first 3 weeks underground in a breeding burrow, and at 4 weeks of age begin moving with the group and eating solid food (Clutton-Brock et al. 1999a). For the next 8 weeks, group members provide the pups with prey items, and the pups encourage this behaviour by giving begging calls while following foraging animals (Manser & Avery 2000). Pups are weaned at approximately 6 weeks of age, but remain entirely dependent on provisioning by group members until at least 10 weeks of age (Brotherton et al. 2001).

All meerkats included in this study were habituated to close observation and handling and were individually marked with permanent marker pen on the tail, or with a small patch of lightly trimmed fur. These marks, which allowed rapid identification, were unobtrusively applied while the animals stood sunning in the mornings.

2.3.2 Behavioural data

A detailed description of the behavioural components of social play in meerkats can be found in Wemmer & Flemming (1974) and a summary is provided in Section 1.5.4. In the present study, I defined social play as that involving mutual bodily contact between two or more animals (described by Wemmer & Flemming as wrestling, clasping, grappling, and mounting). Locomotory and object play were rare, and I excluded them from the analysis because they were used primarily to initiate social play, and their 'playfulness' was sometimes ambiguous.

Meerkat groups emerge from their sleeping burrow soon after sunrise. The animals spend the next 15-90 minutes (mean 37 minutes) around the burrow mouth, sunning, allo-grooming, playing, resting, or excavating the burrow, before setting off to forage. I recorded play behaviour during this period, when play occurs most reliably, using one/zero scan sampling (Martin & Bateson 1986), noting every 20 seconds whether each pup in a litter had played or not during the preceding 20 seconds. I began sampling once all the pups had emerged from the burrow in the morning, and ceased once the group began to forage. In the following analysis, I express one/zero scan data as both a percentage of sample intervals in which a pup played (referred to as rate of play at the burrow) and as the total number of sample intervals in which a pup was seen to play (referred to as extent of play at the burrow). However, these one/zero scan scores are not a true measure of frequency or duration of play, but rather provide an index to the amount each individual played, which proved unobtainable using other sampling methodologies.

I used parametric statistical tests throughout the analysis except where the data differed significantly from normal (based on the Kolmogorov-Smirnov test for normality). In these cases, I used equivalent non-parametric tests. All statistical tests were two-tailed, with a significance threshold of 0.05. Means are given +/- one standard error.

2.3.3 Weight data

All meerkats included in the study could be weighed by enticing them, with a crumb (< 0.5g) of boiled egg, to stand on a tray attached to an electronic balance. The animals were weighed in the morning, before they left the burrow to forage, and again in the evening after they returned to their sleeping burrow. Weights of pups at 4 and 10 weeks of age were obtained in the morning before they began foraging. I used daily weight gain (from morning to evening) as a measure of daily food consumption in weaned pups (those 6-12 weeks of age) from nonexperimental litters and expressed this as a percentage of the individual's morning weight, to allow a comparison of animals of different ages. Daily weight gain was measured on 31 separate days, resulting in a total sample of 142 days for the 39 pups (mean 3.8 +/- 0.3 per individual). To obtain values for the litter, I averaged the daily weight gain of littermates on each particular day.

To analyze variation between individuals within a litter, I expressed each pup's weight (or daily weight gain) as a deviation from the litter's mean weight (or weight gain) by dividing an individual's weight by the litter's mean weight.

2.3.4 Nonexperimental litters

To document play under natural (nonexperimental) conditions, I collected one/zero scan data for 40 meerkat pups (19 females and 21 males) aged between 4 and 10 weeks of age, from ten nonexperimental litters in seven groups. On average, 12 mornings of data were collected for each pup (minimum eight), and these daily scores (both of the number and the proportion of scan intervals in which the individual played) were averaged for each individual. As there was no difference between the sexes in rates of play (*t* test: t_{288}=0.37, P=0.710), I did not separate data for the sexes for any of the analyses. I averaged the scores of individual pups to obtain mean one/zero scores for the litter. Mean litter size was 4.0 +/- 0.5 with a range of one to six pups (one litter of one pup, one of two, one of three, three of four, two of five and two of six). There was no correlation between the amount a litter played and litter size (Pearson correlation: rate: r_8=0.527, r^2=0.278, P=0.117; extent: r_8 =-0.225, r^2=0.023, P=0.697) or group size (Spearman rank correlation: rate: r_S=-0.312, r^2=0.097, N=10, P=0.365; extent: r_S=0.514, r^2=0.264, N=10, P=0.116).

To examine variation in play rates between individuals within a litter, I divided each individual's one/zero score by the mean score for its litter, producing a measure of an individual's deviation from the litter mean (hence a value of one equals the mean). All references to analyses of 'within litter' use an individual's deviations from the mean. Because one of the ten litters of pups included in this study was comprised of only a single pup, I excluded this animal from all analyses of within-litter variation.

2.3.5 Long-term provisioning experiments

I undertook a long-term (4-week) provisioning experiment with 12 litters of pups, from seven groups. After pairing individuals within the litter (based on sex, where possible), I randomly allocated experimental status to one member of the pair. Data were collected on 19 matched pairs of pups. Experimental pups were provided with 12 grams of boiled egg twice daily for 4 weeks, from 4 to 8 weeks of age. The pups were fed at the completion of the morning's data collection period (usually after the group had been foraging for 3 hours) and again in the evening, once the group had returned to their burrow for the night. To ensure that only experimental animals were provisioned, the target animal was provided with its food on a tray (similar to that used for weighing). Once the animal had climbed on to the tray, it was lifted up, and held beyond the reach of other group members.

For experimental litters, I used instantaneous scan sampling (Altmann 1974), at 10-minute intervals, to record the frequency of play and begging behaviour when the group was away from the burrow. Scan data were collected for approximately 3 hours each morning (starting once the group left their sleeping burrow), and again for approximately 1 hour before the group returned to the burrow in the evening. This scan sampling was undertaken for nine of the 12 provisioned litters (14 pairs of pups from six groups), with an average of 38 hours of scan data collected per litter. I also undertook one/zero scan sampling at the burrow for five of the 12 provisioned litters (eight pairs of pups from five groups) with an average of 4.6 mornings of data collection per litter.

During the 8-week period after the completion of this long-term provisioning experiment, I collected instantaneous scan data on 10 of the matched pairs of pups (from seven litters in five groups) to establish whether differences in play rate were maintained. On average, 41 hours of scan data were collected on each pair of pups.

I also undertook a second provisioning experiment, using subadult meerkats (6-12 months of age) and adult meerkats (over 12 months of age). Nondominant group members (see Clutton-Brock et al. 1998a for a definition of dominance) were paired by age, and one member of the pair was randomly allocated experimental status. The experimental regime for adult and subadult meerkats was the same as for pups, except the older animals were given

25g of boiled egg twice daily, and were fed for a period of eight weeks. During this 8-week provisioning period, I used instantaneous scan sampling to record the frequency of play and allogrooming. Scan data were collected for 11 matched pairs of subadults from five groups (averaging 72 hours of scan data for each pair), and 11 matched pairs of adults from five groups (averaging 56 hours of data for each pair).

2.3.6 Short-term provisioning experiment

I undertook a short-term (four-day) feeding experiment with eight litters of pups, in seven groups, when they were between four and 10 weeks of age. On the first day of the experiment, half the pups in the litter were provided with 12.5g of boiled egg. The pups were fed in the morning before the group set off from the burrow to forage. On the second day, the other half of the litter was provisioned in the same way, and on the third and fourth day, the whole procedure was repeated. I undertook instantaneous scan sampling (10-minute intervals) to record the frequency of begging behaviour and play, for a 2.5 to 3 hour period after the group left the burrow to forage. Scan data were pooled for all experimental pups, and all control pups, on a daily basis, and then these daily rates of begging and play behaviour were averaged to obtain values for the litter.

2.4 RESULTS

2.4.1 Weight

There was no consistent relationship between an individual pup's weight and its rate of play. At 4 weeks of age, when the pups first began eating solid food, there was considerable variation in weight of individuals (125 +/- 3.5 g, range 90-166 g, N=40) due to the presence of allolactating females within some groups. Five of the nonexperimental litters (16 pups) were suckled by three to four lactating females, and these pups were 12% heavier than the 24 individuals (from five litters) that were suckled solely by their mother (Mann-Whitney U test: U= 119.5, N_1=16, N_2=24, P=0.045). Despite this variation, there was no correlation between the weight of pups at 4 weeks of age and the rate or extent of their play at the burrow during the next 6 weeks, either within litters (Pearson correlation: rate: r_{37}= -0.146, r^2=0.021, P=0.376; extent: r_{37}= -0.17, r^2=0.029, P=0.3) or between litters (Pearson correlation: rate: r_8= -0.502, r^2=0.252, P=0.139; extent: r_8 =0.286, r^2=0.082, P=0.422).

Similarly, weight at 10 weeks of age (311 +/- 4.1 g, range 258-381 g, N=40) was not correlated with either rate or extent of play at the burrow during the preceding 6 weeks for litters (Pearson correlation: rate: r_8= -0.064, r^2=0.004, P=0.860; extent: r_8=0.262, r^2=0.069, P=0.465), but was correlated with rate of play within litters (Pearson correlation: rate: r_{37}=0.418, r^2=0.175, P=0.008; extent: r_{37}=0.377, r^2=0.142, P=0.018).

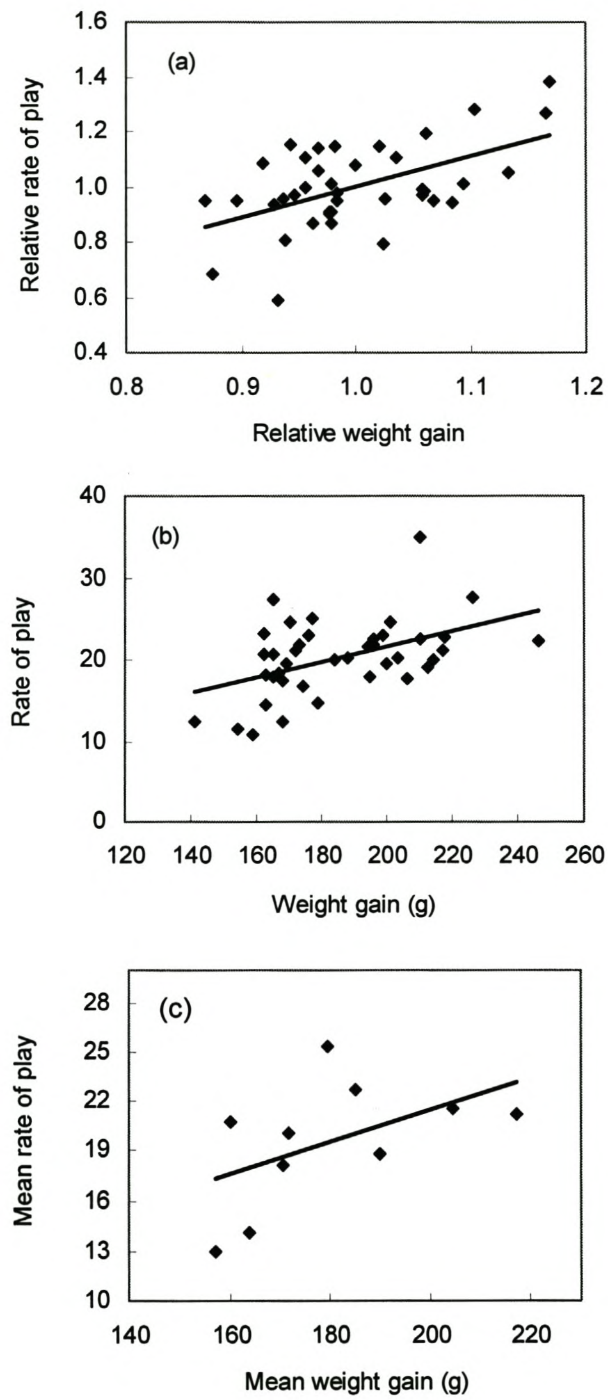
2.4.2 Long-term weight gain

Weight gain over the 6-week period (185 +/- 3.7 g, range 141-247 g, N=40) was positively correlated with rates of play. Within litters, there was a significant positive correlation between the relative amount of weight a pup gained between the ages of 4 and 10 weeks and both its relative rate, and relative extent, of play at the burrow over the same 6-week period (Pearson correlation: rate: r_{37}=0.553, r^2=0.306, P<0.001; extent: r_{37}=0.509, r^2=0.259, P=0.001). Weight gain explained 31% of the variation in rates of play between littermates (Fig. 2.1a), 23% of variation in rates between all individuals (Pearson correlation: r_{38}=0.474, r^2=0.225, P=0.002, Fig. 2.1b) and 26% of variation in rates between litters, although this last correlation was not statistically significant (Pearson correlation: r_8=0.516, r^2=0.266, P=0.127, Fig. 2.1c).

2.4.3 Daily weight gain

There was no relationship between the mean rate or extent a litter played at the morning sleeping burrow and the mean amount of weight the pups had gained during the previous day (Spearman rank correlation: rate: r_S=0.195, N=31, P=0.293; extent: R=0.343, r_S=1.966, N=31, P=0.059), nor was there any correlation within litters (Spearman rank correlation: r_S=0.095, N=147, P=0.254). While both the rate and the extent of play showed a positive relationship with prior weight gain for individuals (Spearman rank correlation: rate: r_S=0.200, N=147, P=0.015; extent: r_S=0.275, N=147, P=0.001), the correlation was weak, with weight gain explaining only 4% of the variation in rate of play. Therefore, the amount of food consumed by an individual pup during the day did not affect the amount the individual played the following morning.

Figure 2.1. Rate of play at the burrow (percent of one/zero scans that included play) as a function of weight gain, in pups aged 4-10 weeks, for (a) individuals within a litter (deviation from the litter mean; N=39 pups in nine litters); (b) individuals (N=40); and (c) litters (N=10).



2.4.4 Long-term provisioning experiments

Pups provided with supplementary food over a 4-week period gained an average of 185 +/- 8.0 g (range 133-255 g) during the experiment compared with 135 +/- 7.6 g (range 81-192 g) for the unfed controls (paired *t* test: t_{18}=7.78, P=<0.001). Provisioned pups played significantly more frequently than the unfed controls, with fed pups spending 4.9% of their time in play (as measured by instantaneous scan sampling) compared with 3.0% for the control pups (paired *t* test: t_{13}=3.484, P=0.004, Fig. 2.2). They also spent a significantly lower percentage of time begging for food (46%) than their unfed peers (56%; paired *t* test: t_{13}=6.22, P=<0.001).

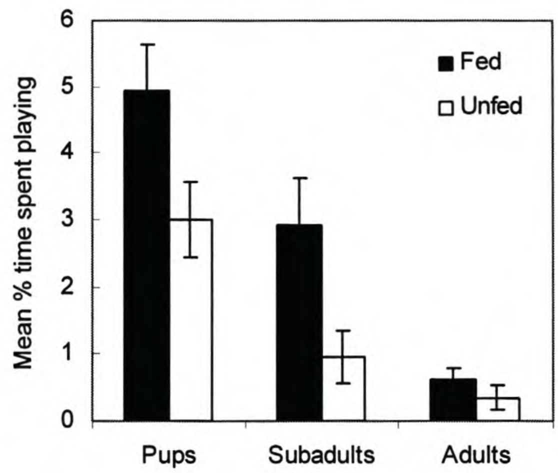
Fed pups also played significantly more than unfed controls at the morning sleeping burrow when the group was not foraging (Wilcoxon matched-pairs test: extent: T=3.0, N=8, P=0.036; rate: T=1.0, N=8, P=0.017). On average, fed pups played during 26 one/zero scan intervals (26.9% of scan intervals) compared with 18 (17.7%) for unfed controls. The one/zero scores for unfed pups within provisioned litters did not differ significantly from those of pups in nonprovisioned litters (Mann-Whitney *U* test: extent: W=138.0, N_1=40, N_2=8, P=0.112; rate: W=145.0 N_1=40, N_2=8, P=0.162).

As with pups, fed subadult meerkats (6-12 months of age) played significantly more than unfed controls, devoting 2.9% of their time to play as compared with 0.9% for their unfed peers (Wilcoxon matched-pairs test: T=1.0, N=11, P=0.004, Fig. 2.2). A similar, but nonsignificant, trend was observed for adult meerkats (over 12 months of age) with fed adults playing 0.6% of their time and unfed controls 0.3% (Wilcoxon matched-pairs test: T=1.0, N=11, P=0.128, Fig. 2.2).

The frequency of allogrooming did not differ between fed adults and their unfed controls (both 0.3%; (Wilcoxon matched-pairs test: T=11.0, N=11, P=0.612). Allogrooming occurred too infrequently in subadult meerkats (and pups) to allow an effective comparison.

During the 8-week period after provisioning, the rate of play in provisioned pups did not differ significantly from that of unfed controls (3.1% compared with 3.0% respectively; paired *t* test: t_9=0.560, P=0.589).

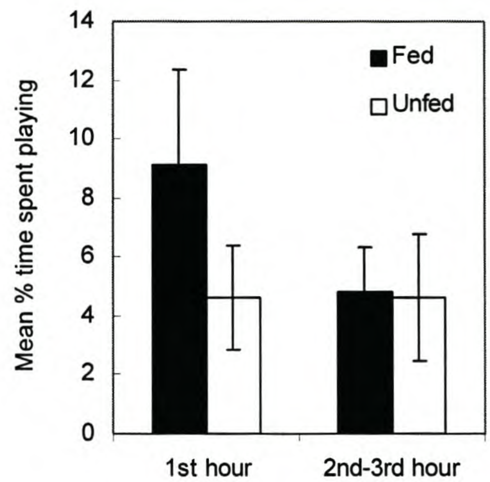
Figure 2.2. Long-term provisioning experiment: rate of play (instantaneous scan sampling) in fed animals and unfed controls, by age class. (Pups=1-3 months old, N=14 pairs; subadults=6-12 months old, N=11 pairs; adults>12 months old, N=11 pairs.) Vertical lines indicate SE.



2.4.5 Short-term provisioning experiment

Pups provided with supplementary food before the group began to forage in the morning spent no more time playing during the morning than their unfed siblings (Wilcoxon matched-pairs test: T=7.0, N=8, P=0.123). However, during the first hour after provisioning, the fed pups did play significantly more than the controls, spending 9.1% of the hour in play compared with 4.6% for the controls (Wilcoxon matched-pairs test: T=3.5, N=8, P=0.042, Fig. 2.3). During this initial hour, the fed pups also spent significantly less time begging for food than the controls (63.1% versus 76.0%, as measured by instantaneous scan sampling; paired t test: t_7=5.774, P=0.001). However, during the remainder of the morning (the second and third hour after provisioning), the effect of feeding wore off, and there was no significant difference between fed and unfed pups in either their frequency of play (Wilcoxon matched-pairs test: T=7.0, N=8, P=0.893) or begging behaviour (paired t test: t_7=1.690, P=0.135). Fed pups played 4.8% of the second and third hour, compared with 4.6% for the controls, and begged 66.9% of the time compared with 71.6% for controls (Fig. 2.3).

Figure 2.3. Short-term provisioning experiment: rate of play (instantaneous scan sampling) in fed pups and unfed controls in the first, and second to third hour after feeding (N=8 litters). Vertical lines indicate SE.



2.5 DISCUSSION

Variation in food consumption had a significant effect on the frequency of play in young meerkats. Long-term nutritional status (as measured by weight gain over a 6-week period) was positively correlated with rate of play, not only among pups from different litters and groups but also among littermates, which are not subject to variations in territory quality or the number of helpers in the group. Although weight gain accounted for only one-quarter to one-third of the variation observed in rates of play, these data were collected during a year of unusually high rainfall (465 mm compared with an annual average of 250 mm). Prey abundance was correspondingly high, and none of the subjects were facing any food shortage.

The correlation between long-term weight gain and play detected under natural conditions might not have been causal since, for example, unhealthy pups, or those carrying a heavy parasite load, might exhibit less growth and less play. However, the causality of the relationship was confirmed by the long-term provisioning experiments. The experimental animals, whose nutritional status was raised artificially through prolonged provisioning, played at least 50% more than the nonprovisioned controls.

While long-term nutritional status influenced rates of play, short-term variations in food consumption did not. The amount of food a pup consumed during the day did not predict how much it played the next morning, even though food consumption could vary greatly from day to day (e.g. if the group was prevented from foraging by the presence of a predator or interactions with a neighbouring group). The short-term provisioning experiment demonstrated that the behavioural changes caused by a single good meal were highly transitory. Freed from the need to beg for food, the satiated pup more than doubled its rate of play during the first hour after provisioning, but its behaviour rapidly returned to normal once its satiation wore off.

Pup weight, at 4 and 10 weeks of age, showed only partial correlation with rates of play because it did not provide an accurate measure of an individual's current nutritional status. This was clearly shown by the after-effects of the long-term provisioning experiment. Once provisioning ceased, the rate of play of fed pups dropped to normal levels, even though they remained heavier than their unfed controls until at least 6 months of age (Clutton-Brock et al. 2001c).

Notably, weight at 4 weeks of age was not correlated with subsequent rates of play. In meerkats, approximately 50% of all litters that emerge from the burrow are suckled by more than one female (Clutton-Brock unpublished data). Since the amount of milk produced by lactating females is not related to the number of lactating females in the group, or the number of pups (White 2001), the presence of allolactators has a major effect on the amount of milk available to individual pups. Because young meerkats live almost exclusively on milk until 4 weeks of age, their weight at this age can serve as an index of milk availability. For example, in this study, pups raised with allolactators were 12% heavier than those suckled solely by their mother. Nevertheless, these variations in milk availability were not correlated with subsequent rates of play, as might be expected from the findings of studies of domestic kittens, in which disruptions or reductions in milk availability (Bateson & Young 1981), short-term interruptions to lactation (Bateson et al. 1981; Martin & Bateson 1985b) and food rationing of mothers (Bateson et al. 1990), all resulted in an increase in the kittens' subsequent rate of play. Bateson et al. (1990) suggested that the kittens perceived these variables as cues that their mother was experiencing a food shortage, and accelerated their development to ensure adequate play experience before being forced to curtail play at weaning. However, in a co-operative species such as the meerkat, in which all group members assist in provisioning the young, it is unlikely that a pup could use milk availability as an indicator of future food abundance.

While the long-term provisioning experiment showed that raising the level of nutrition resulted in an increase in play, we cannot assume that this relationship was caused by energetic factors. One alternative explanation is that the provisioned meerkat pups were merely accelerating their rate of development to exploit favourable conditions, which might be expected of a desert-adapted species subject to highly ephemeral conditions. Since the rate of play in meerkats normally peaks at around 12 weeks of age (Fig. 6.1), acceleration in the development of 4 to 8-week-old pups would result in an increase in play such as that observed in the long-term provisioning experiment. However, if an increase in rate of development was responsible for the experiment's result, the rate of play in fed pups during the 8-week period after the provisioning experiment (at 8-16 weeks of age) should have been appreciably lower than that of their unfed peers. This was not the case, with both ex-fed and unfed pups playing at the same rate. Similarly, if changes in the rate of play of fed subadult meerkats (6-12 months of age) were due to accelerated development, their play should have decreased, relative to the controls, rather than trebled.

It is also conceivable that changes in the pups' social environment led to the differing rates of play observed within provisioned litters. Fed pups were 21% heavier than their controls by the conclusion of the experiment, and this size difference may have inhibited play in the unfed pups. Several studies of primates and ungulates have found that individuals avoid play fighting with partners which they are unable to beat (Owens 1975b; Byers 1980; Biben 1998) and as a consequence preferred play partners are often closely matched for age and size (Thompson 1996; Berger 1980; Stevenson & Poole 1982; Watson 1993). However, the rate of play of unfed pups was no lower than that of pups from nonprovisioned litters, and differences in rate of play between fed and unfed pups were not maintained once provisioning ceased, even though the disparity in weight was maintained for many months after the experiment (Clutton-Brock et al. 2001c).

Artificially providing animals with food freed them, to some extent, from the necessity of foraging or begging for food. This additional spare time, rather than any energetic considerations, could have caused the increase in play in the fed animals. The accessibility of food (and consequently altered time budgets) appears to have been an important factor in several studies of play. Lee (1984) found that the increase in the rate of play of young vervet monkeys, during the wet season, was not only correlated with quality of diet, but also with a decrease in time spent foraging and an increase in the frequency of all social interactions during this time to indulge in play. Thus the observed increase in rates of play could not be explained simply by fed pups having additional free time.

The energetic benefits of provisioning played a major role in increasing the rate of play. While the frequency of play more than doubled in response to long-term provisioning in all age classes of meerkat, the frequency of allogrooming (in adults) showed no change. Like play, social grooming is undertaken during nonforaging periods, and has been attributed with many of the social benefits (Dunbar 1991) also attributed to play (Poirier & Smith 1974). However, unlike play, allogrooming does not involve high levels of physical exertion. Lee (1984), working with vervet monkeys, also found that rates of social grooming did not vary with food availability, despite significant changes in energy intake, proportion of time spent foraging and rates of play, across the seasons. She attributed this to the low energetic costs of social grooming. The finding by Clutton-Brock et al. (2000; 2001a) and Brotherton et al. (2001) that provisioned adult meerkats significantly increased the amount they undertook energetically costly helping behaviours (such as pup-feeding and babysitting), also supports the argument that play, like helping behaviour, is of high energetic cost.

Barber (1991) has suggested that, despite this energy expenditure, play is not costly to an organism because only energy 'in excess of need' is used in play. He proposed that the function of play is to provide adaptive energy loss (mediated by the sympathetic nervous system and brown adipose tissue) to prevent obesity (as an antipredator strategy), balance a low-protein diet in favour of growth, and increase resistance to pathogens and cold exposure. Although provisioned meerkats played more frequently, as predicted by Barber's energy regulation hypothesis, White's (2001) finding that provisioned pups also showed a significant increase in body condition (not just weight) compared with their unfed controls suggests that obesity avoidance is not the primary function of meerkat play. Nunes et al. (1999) came to a similar conclusion after finding that provisioned ground squirrels became significantly fatter than controls, despite increased rates of play. Fatter, provisioned meerkat pups were no more likely to suffer predation than their leaner, unfed siblings (Clutton-Brock et al. 2001c), despite intense predation and a mean annual mortality rate of 38% for juveniles in this population (Clutton-Brock et al. 1999a). Similarly, dietary protein is not likely to be limiting in young meerkats which feed almost exclusively on protein-rich arthropods and vertebrates (Brotherton et al. 2001). Barber's hypothesis also predicts that frequency of play should be inversely related to both ambient temperature and fat acquisition. However, rates of play in meerkat pups showed no correlation with temperature (L. Sharpe, unpublished data), and White (2001) found that body condition in meerkats (from nonexperimental litters) rose steadily between the ages of 7 and 15 weeks, the period during which play was most frequent (Fig. 6.2). Renouf (1993) made a similar finding when comparing play and seasonal fat accumulation in captive harbour seals (*Phoca vitulina*).

While the cost of dedicating energy to play remains unclear, the consequences of such energy expenditure are likely to be far greater for a meerkat pup than for a full-grown adult. The energy a pup expends on play is likely to have been diverted from growth, and Clutton-Brock et al. (2001c) found that large pups enjoyed considerable advantages over small ones, later in life. Animals which were relatively heavy at 12-16 weeks of age were more successful at catching prey, contributed more to cooperative activities, were more likely to breed within their natal group (if female), and were more likely, than their siblings, to become dominant breeders. Consequently, play in meerkats is not only energetically costly, but it must also offer considerable adaptive advantages to the individual if these costs, in terms of future lifetime reproductive success, are to be offset.

CHAPTER THREE

SOCIAL PLAY DOES NOT REDUCE AGGRESSION IN WILD MEERKATS

(*Animal Behaviour*, 2003, 66, 989-997)

3.1 ABSTRACT

Of the numerous hypotheses advanced to explain the adaptive significance of play, several assert that social play increases social harmony, cementing alliances and reducing aggression between group members or littermates. These hypotheses are frequently cited, but their validity remains unknown. This study examined the relationship between social play and aggression in juvenile meerkats, *Suricata suricatta,* living in a wild population in the southern Kalahari desert. I tested the hypothesis that social play reduces aggression, by examining rates of play, play partner choices, the structure of social play and rates of aggressive interactions during foraging. I found no relationship between frequency of play and level of aggression, either between individuals or during the course of development. Pups that played together frequently were just as aggressive toward one another as pairs of pups that played infrequently, and play interactions had no subsequent effect on the likelihood of aggression. In contrast, aggressive interactions during foraging inhibited the subsequent likelihood of play, and high levels of aggression during foraging changed the structure of social play, with victimized pups avoiding play wrestling. I conclude that social play does not reduce aggression in young meerkats.

3.2 INTRODUCTION

Several decades of research into the adaptive significance of play have led to the postulation of numerous hypotheses of its function (Fagen 1981; Smith 1982; Baldwin 1986). A number of these propose that play increases social harmony, for example strengthening social bonds, cementing alliances or reducing aggression between group members or littermates. Such explanations for play have been postulated in studies of a diverse range of mammals, including carnivores (Bekoff 1974; West 1974; Poole 1978; Drea et al. 1996), rodents (Panskepp 1981; Waterman 1988; Pellis et al. 1993; Holmes 1995), primates (Carpenter 1934; Hausfater 1972; Poirier & Smith 1974; Sugiyama 1976; Lee 1984), artiodactylids (Byers 1984) and carnivorous marsupials (Soderquist & Serena 2000). Yet despite the popularity of these hypotheses, it is still not known whether play does reduce aggression, or increase social harmony, between playing individuals.

The proposition that social play functions to strengthen social bonds was supported by early speculation that interspecific variation in play was positively correlated with level of sociality (Poirier & Smith 1974; Bekoff 1977a). However, there is now evidence that play and sociality are not related, at least in canids and rodents (Biben 1983; Pellis & Iwaniuk 1999). The strongest support for the hypotheses is provided by the distribution of play during development in captive animals. Drea et al. (1996) found that rates of social play in captive, infant spotted hyaenas, *Crocuta crocuta,* rose steadily as rates of sibling aggression fell, peaking at the age at which the cubs would normally integrate with others in the pack. They concluded that social play contributed to the termination of serious aggression and promoted social cohesion. In solitary carnivores, such as polecats, *Mustela putorius* (Poole 1978), domestic cats, *Felis catus* (West 1974), and chuditch, *Dasyurus geoffroii* (Soderquist & Serena 2000), rates of play in captive individuals decline markedly at the age at which littermates disperse in the wild. Researchers working on these species have suggested that play may serve to reduce the aggression that these animals normally exhibit toward conspecifics, so that young littermates can cohabit without inflicting injury upon one another. However, Watson (1993) found no relationship between rates of aggression and social play in captive red-necked wallabies, *Macropus rufogriseus banksianus*, and studies of free-ranging primates have detected no adverse effect upon social relationships of reductions in social play caused by food shortage or poor habitat quality (Baldwin & Baldwin 1974; Lee 1984).

This study examines the relationship between social play and aggression in juvenile meerkats, *Suricata suricatta,* in a wild population in the southern Kalahari Desert. Meerkats are social, cooperative mongooses that live in groups of up to 40 individuals. Under favourable conditions, groups can rear up to four litters of pups annually (mean litter size is four) and all group members provide the pups (aged 4-10 weeks) with food (Clutton-Brock et al. 1999a). Meerkat pups promote this provisioning behaviour by begging noisily (Manser & Avery 2000) and, because adults preferentially feed the nearest pup (Brotherton et al. 2001), they compete aggressively for proximity to foraging group members. The pups display 'scramble competition' (White 2001) rather than establishing a fixed dominance hierarchy, so aggressive interactions occur between all littermates and are not limited to asymmetrical demonstrations of dominance or submission (Bernstein 1981). This provides an unparalleled opportunity to assess the relationship between aggression and social play. The advantages of undertaking such a study on a wild population, cannot be overemphasized, considering that both play and aggression are strongly influenced by a number of factors badly distorted by captivity, such as the availability and distribution of food (Lee 1984; Sharpe et al. 2002), type of terrain (Berger 1980; Stevenson & Poole 1982), density of individuals and group composition (Lee 1984; Biben 1998).

This study tested four predictions generated by the hypothesis that social play serves to reduce aggression in young meerkats. These predictions are (1) a negative correlation between frequency of play and frequency of aggression, for individual pups and litters; (2) a negative temporal relationship between rate of play and rate of aggression during development; (3) pairs of pups that frequently play together will show less aggression towards one another than pups that play together infrequently; and (4) pups that have just shared a play bout will be less likely to behave aggressively toward one another than those that have not played together.

3.3 METHODS

3.3.1 Study population

I undertook the study between August 1999 and November 2000, working on a natural population of meerkats living on ranchland in the southern Kalahari desert, 30 km west of Van Zylsrus, South Africa (26°58'S, 21°49'E). See Section 1.6 for details of the study site's topography, vegetation and rainfall. The study was carried out under a license issued by the Northern Cape Conservation Service, South Africa. I collected most of the data on eight main study litters (40 individuals) from seven meerkat groups, when the pups were 4-10 weeks old.

Two of these eight litters were comprised of pups borne by more than one female, but these pups were reared together as a single litter, and the age difference between the pups was not greater than 2 weeks. I also collected supplementary data from five additional litters of pups (24 individuals; Table 3.1).

All meerkats included in the study were habituated to close observation and handling, and each had been individually marked on the tail (with coloured permanent marker pen) while it stood sunning at the burrow.

Table 3.1. Data collection regime for the study litters.

		Social foraging aggression (focal animal data)		Rate of play (one/zero scans at morning burrow)					Play partners (ad libitum)
Litter	Litter size	4-6 weeks	6-10 weeks	3-4 weeks	4-6 weeks	6-10 weeks	10-16 weeks	16-26 weeks	4-10 weeks
Main litters									
VL9903	6	x	x	x	x	x	x	x	x
VW9905	3	x	x	x	x	x	x	x	x
VW9906	4	x	x	x	x	x	x	x	x
VE0001/3	9	x	x	x	x	x	x	x	x
VD9904	5	x	x		x	x	x	x	x
VF9907	6	x	x		x	x	x	x	x
VV0003	4	x	x		x	x	x	x	x
VY0002/3	3	x	x		x	x			x
Supplementary litters									
VD9905	5		x						x
VY9907/8	5			x					
VV9904/5	7			x					
VY9910	5			x					
VL9902	2			x					

3.3.2 Weight

Individual pups were weighed each morning before they began foraging, by enticing them on to an electronic balance with a crumb (<0.5g) of hardboiled egg. To calculate weight differences between individuals within a litter, I divided the 6-week study period into three 2-week blocks. For each 2-week period, I averaged a pup's morning weight, and expressed the difference between its mean weight and that of each of its littermates as a percentage of the pair's mean weight. The percentage differences obtained in each of the three 2-week blocks were then averaged to obtain a value for each dyad for the whole 6-week study period.

3.3.3.Social play

Although social play is a prominent feature of meerkat behaviour, it accounts for only 3.0% of a pup's waking hours, and 0.3% of an adult's (Chapter 2). Play normally occurs only when group members are gathered together at a burrow entrance (i.e. early in the morning, after a predator scare, during the midday rest period in the hotter months of the year or at dusk), and its occurrence is both highly sporadic and unpredictable. These characteristics made it infeasible to use conventional sampling methodologies when quantifying individual rates of play. The rarity of play precluded instantaneous scan sampling (Altmann 1974), because an impossibly large sample would have been needed to document the small differences between littermates, and focal animal sampling (Altmann 1974) was impractical because of the highly sporadic occurrence of play (normally only a few minutes of highly intense play activity, by most of the group, interspersed with hours of nonplay). I therefore chose to use one/zero scan sampling (Martin & Bateson 1986) to document the relative frequency of social play shown by individual pups, using a sample interval of 20 seconds (i.e. I recorded every 20 seconds whether each pup in the litter had played or not during the preceding 20 seconds). I defined social play (also referred to as play fighting) as play involving mutual bodily contact between two or more animals. I collected one/zero scan data after the meerkat group emerged from its sleeping burrow around sunrise (beginning when the whole litter had emerged) and stopped sampling when the group set off to forage, usually 15-90 minutes (mean 37 minutes) later. I targeted this period at the morning burrow because it is the time at which meerkats play most reliably. I collected one/zero scan data for the eight main study litters (40 pups), averaging 12 mornings of data for each pup (minimum eight), between the ages of 4 and 10 weeks. To compare rates of play with foraging status, I continued collecting one/zero scan data until the pups were 6 months of age (minimum of four mornings per month), in seven of the eight study litters. I also obtained one/zero scan data for eight litters (four of the study litters, plus four additional litters; see Table 3.1) before they began moving with the group (when 3-4 weeks of age).

To quantify which individuals played together, in 4 to 10 week old pups, I documented individual play bouts ad libitum (Altmann 1974) whenever play was observed. Individual bouts of social play were generally very short, with only 2.5 +/- 0.3% of a pup's play fights lasting more than one minute. I considered a bout to have concluded if a pair ceased playing for longer than 5 seconds. I recorded the identity of the play partners as a dyad, and although additional meerkats took part in 16 +/- 0.7% of an individual's play bouts, the two main protagonists were clearly identifiable because of the one-on-one nature of the play. I also documented the main behavioural components of the play bout (see Section 1.5.4 for a detailed description of these components), recording all observed occurrences of: (1) wrestling (one animal lies on its back while the other stands on or over it, pinning it to the ground); (2) grappling (animals stand bipedally, clasping each other with their forelegs and attempting to push one another over); (3) mounting/being mounted; and (4) chasing/fleeing. I documented play bouts in all eight study litters, plus one additional litter (VD9905; Table 3.1), resulting in a sample of 45 individuals. Only play bouts undertaken with a littermate (89% of a pup's total play interactions) were included in the analysis, resulting in an average of 282 +/- 14.8 play bouts for each pup (range 132-443).

3.3.4 Aggression

At approximately 4 weeks of age, meerkat pups begin travelling with the group and competing with one another for prey items provided by group members (Brotherton et al. 2001). To document the frequency and level of aggression shown by pups while social foraging (begging noisily for food while following a foraging group member), I undertook focal animal sampling (Altmann 1974) for all eight study litters, plus one additional litter (VD9905; Table 3.1), resulting in a sample of 45 individuals. I undertook 15-minute periods of continuous data recording on each littermate (selected randomly) while the litter was actively social foraging. On average, I collected 253 +/- 10.6 minutes of focal animal data per individual. I recorded all social foraging 'encounters' (defined as a littermate entering within a 1-metre radius of the focal animal, provided at least one of the two was actively begging for food), the identity of the encounter's initiator, the level of aggression shown by both pups, and the outcome of the encounter. An encounter was considered to have concluded when the two interactants moved more than 1 meter apart, or both ceased begging for food for a period greater than 5 seconds. Play bouts and items fed to the focal pup were also documented during focal sampling.

I classified social foraging encounters as 'nonaggressive' if the pups ignored one another, simply watched one another or began to play. I classed encounters as 'mildly aggressive' if a pup chose to withdraw after watching its opponent (which might growl, spit or piloerect) and as 'strongly aggressive' if one or both of the pups charged at, chased or fought (defined as physical contact with biting) its opponent. Hourly rates of encounters and aggression were strongly correlated with litter size (and group size in the case of encounters; Table 3.2), so I used the proportion of encounters that involved strong aggression as my standard measure of aggression, because it was unrelated to these variables (Table 3.2).

Table 3.2. Statistical correlations between group or litter size, and social foraging encounters or rate of play.

	Litter size (N=9)		No. group members/no. pups (N=9)	
	r	P	r	P
Hourly rate of encounters *	0.79	0.009	-0.85	<0.001
Hourly rate of strong aggression +	0.78	0.013	-0.63	0.072
% Encounters with strong aggression +	0.38	0.310	-0.18	0.634
Rate of play #	0.33	0.420	-0.46	0.251

* Spearman correlations. + Pearson correlations, df=7. # Pearson correlations, df=6.

To examine the immediate aftereffects of strong aggression, I selected social foraging encounters (strongly aggressive and nonaggressive) that occurred during the first 5 minutes of each focal sample and documented whether each of these was followed, within 10 minutes, by play by the same dyad. To examine whether play reduced the subsequent likelihood of aggression, I used all social foraging encounters that occurred during the last 5 minutes of focal sampling, and documented whether play, by the same dyad, had occurred during the preceding 10 minutes. For both these analyses, I pooled data for individual litter members and calculated percentages by litter, because of the relative rarity of play bouts during foraging.

3.3.5 Analysis

Throughout the analysis I have used 'deviation from litter mean' to standardize individual data derived from different litters. To obtain this measure, I divided the value recorded for each individual by the mean value for its litter (hence a value of one equals the mean). I chose this method of standardization because it corrects for factors that affect the mean (such as litter size, group size and composition, habitat type, territory quality, temperature, prey abundance), but maintains interlitter differences in variance (caused primarily by individual differences between littermates). All references to 'within litter' analyses or 'relative' rates or proportions, refer to deviations from the litter mean.

In the analysis of one/zero scan data, I averaged the daily rates of play for each individual, over the main 6-week study period, and obtained mean litter rates by averaging the rates of individual litter members. To compare rates of play with foraging status, I divided the one/zero scan data collected over the 6 months into five periods, each corresponding to a different foraging status (Fig 3.1), averaged individuals' daily rates of play for each period, and then averaged the values for littermates to produce a mean value for the litter. I used a repeated measures ANOVA to test the relationship between play and foraging status in pups over 4 weeks of age, restricting this analysis to the seven litters whose rates of play were sampled until they were six months of age.

Although I refer to the percentage of one/zero scan intervals in which a pup played as its 'rate' of play, one/zero scan sampling does not provide a true measure of frequency. There was, however, a significant correlation between the relative rates of play obtained using one/zero scan sampling and those derived from an analysis of the ad libitum records of individual play bouts (Pearson correlation: r_{38}=0.780, P<0.001).

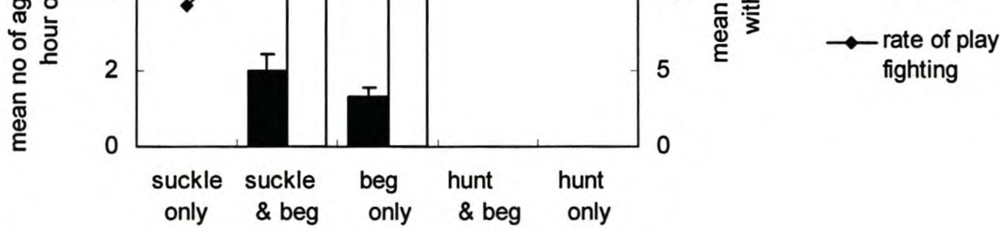
There was no difference between the sexes in rate of play (paired t test: t_7=0.679, P=0.519), rate of encounters during social foraging (paired t test: t_8=-1.398, P=0.200) or percentage of encounters that involved strong aggression (paired t test: t_8=1.012, P=0.341), so I did not separate data for the sexes for any of the analyses. I used parametric statistical tests throughout the analysis, except where the data differed significantly from a normal distribution (based on the Kolmogorov-Smirnov test for normality with a significance threshold of 0.02). In these cases, I used equivalent nonparametric tests. All statistical tests were two-tailed, with a significance threshold of 0.05. Means are given +/- SE.

3.4 RESULTS

3.4.1 Rates of play and aggression

Meerkat pups 4-10 weeks old showed social play during 19.8 +/- 1.4% of one/zero scans at the burrow in the morning (N=8 litters). Although rates increased when pups began foraging with the group, rising from 9.2 +/- 1.5% of scans in 3-4-week-old pups to 15.1 +/- 1.8% in 4-6-week-old pups (t test: t_{14}= -2.519, P=0.025), once the pups were eating solid food, rate of play was not significantly related to foraging status (repeated measures ANOVA: $F_{3,6}$=2.863, P=0.067). Young meerkats played during 21.7 +/- 1.7% of scans as 6-10-week-olds, 20.0 +/- 1.7% as 10-16-week-olds, and 16.6 +/-1.6% as independent foragers aged 16-26 weeks (Fig. 3.1).

Figure 3.1. Mean rate of play and frequency of aggression during social foraging, by foraging status. Suckle only: 3-4 weeks old, not yet accompanying the group or eating solid food (N=8 litters); suckle and beg: 4-6 weeks old, foraging with group (social foraging) and suckling (N=8); beg only: 6-10 weeks old, totally reliant on provisioning by group (N=8); hunt and beg: 10-16 weeks old, catching increasing proportion of own food and social foraging declining (N=7); hunt only: 16-26 weeks old, fully independent (N=7). Vertical lines indicate SE.



During social foraging, a meerkat pup encountered one of its littermates 13.7 +/- 1.1 times per hour (N=9 litters). Of these encounters, 42 +/- 3.1% resulted in aggression (i.e. the withdrawal of a pup) and 36 +/- 2.3% involved strong aggression. The degree of aggression exhibited by young meerkats changed with age. Aggression was never observed in very young pups, but once they began competing for food items at 4 weeks of age, aggressive interactions became frequent. Rate of aggression was highest during the first 2 weeks of the 6-week social foraging period, with pups aged 4-6 weeks showing significantly higher hourly rates of both encounters (19.5 +/- 2.2 versus 12.9 +/- 1.8; paired t test: t_7=6.806, P<0.001) and strong aggression (7.6 +/- 1.1 versus 4.7 +/- 0.6; paired t test: t_7=3.952, P=0.006) than those aged 6-10 weeks (Fig. 3.1). However, there was no difference in the proportion of their encounters that ended in strong aggression (37.0 +/- 2.1% versus 37.0 +/- 3.5%; paired t test: t_7=0.004, P=0.997). Although pups showed occasional begging behaviour and were fed intermittently after 10 weeks of age, aggressive interactions were rare, and it was not feasible to measure their frequency using focal animal sampling.

In 4-10 week old pups, there was no correlation between the proportion of social foraging encounters that ended in strong aggression and rate of play, either between or within litters (between litters: Pearson correlation: r_6= -0.365, P=0.373; within litters: Spearman rank correlation: r_s= 0.000, N=40, P=0.998).

3.4.2 Play partners and aggression

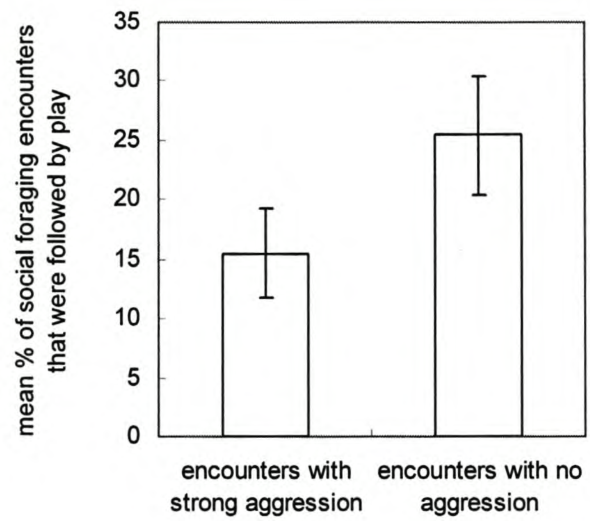
The frequency with which a pair of pups played together was, in general, not related to the level of aggression they displayed towards one another when social foraging. Within litters, the relative number of play bouts shared by a dyad showed no correlation with the relative proportion of the dyad's encounters that ended in strong aggression (Spearman rank correlation: r_s=0.008, N=104, P=0.935), but was positively correlated with the proportion that ended in fights (Spearman rank correlation: r_s=0.194, N=104, P=0.048).

3.4.3 Immediate aftereffects of play and aggression

The level of aggression shown during social foraging did not differ between pairs of pups that had played together during the previous 10 minutes and pairs that had not. Prior play did not affect the percentage of social foraging encounters that ended in strong aggression (paired t test: t_8= -1.315, P=0.225). However, pairs of pups that had experienced strong aggression in a social foraging encounter were less likely to play with one another during the subsequent

10 minutes than pairs that had encountered one another without aggression (paired t test: t_8= -2.62, P=0.031). Play took place after 25.4 +/- 5.0% of nonaggressive foraging encounters, compared with only 15.5 +/- 3.7% for encounters with strong aggression (Fig. 3.2).

Figure 3.2. Mean percentage of social foraging encounters that were followed within 10 minutes by play with the same partner. Vertical lines indicate SE.



3.4.4 Behavioural composition of play fights

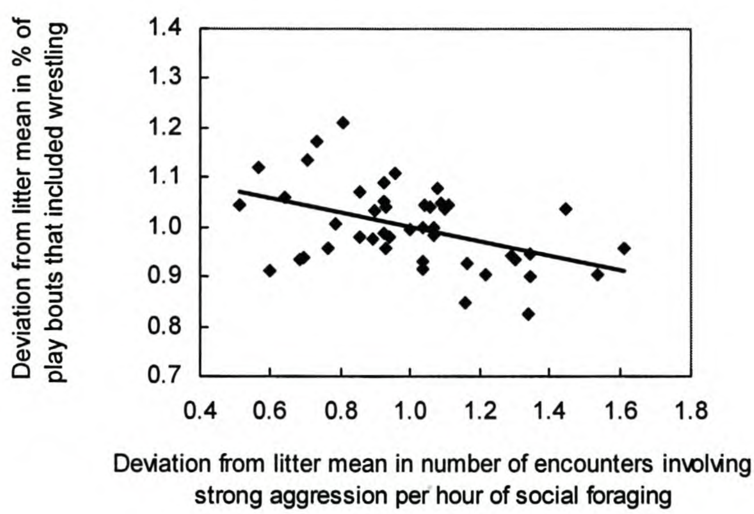
The behavioural content of play fight bouts differed for individuals that suffered higher levels of aggression than their littermates (Fig. 3.3). Within litters, there was a negative correlation between the relative proportion of a pup's play fights that included wrestling and the relative rate of strong aggression that littermates directed towards that pup (Pearson correlation: r_{43}= -0.383, P=0.009), but not the relative rate of strong aggression that the pup directed towards its littermates (Pearson correlation: r_{43}= -0.185, P=0.223). There was also no relationship between the relative proportion of a pup's play bouts that included wrestling and its relative weight (Pearson correlation: r_{43}=0.203, P=0.18).

There was no relationship between subjection to strong aggression and the likelihood of wrestling for individual dyads. The relative proportion of a dyad's play bouts that included wrestling was not correlated with the relative proportion of the pair's social foraging encounters that ended in strong aggression (Spearman rank correlation: r_s=0.057, N=104,

P=0.568), nor with the relative weight difference between members of a dyad (Pearson correlation: r_{102}=0.079, P=0.423).

None of the other behavioural components of play fighting that were documented in this study (grappling, chasing/fleeing and mounting/being mounted) were correlated with aggression during social foraging.

Figure 3.3. Relative rate of strong aggression during social foraging as a function of the relative likelihood of wrestling while play fighting, within litters (Pearson correlation: r_{43}= -0.456, P=0.002).



3.4.5 Level of nutrition

There was no correlation between the mean number of feeds a pup received per hour of social foraging and the proportion of its social foraging encounters that ended in strong aggression (between litters: Pearson correlation: r_7= -0.025, P=0.949; within litters: Spearman rank correlation: r_s=0.151, N=45, P=0.322). Similarly, aggression was not correlated with a pups' weight gain over the 6-week social foraging period (between litters: Pearson correlation: r_7= -0.049, P=0.9; within litters: Spearman rank correlation: r_s=0.068, N=45, P=0.658). In contrast, rate of play was positively correlated with weight gain over the 6-week social foraging period (between litters: Pearson correlation: r_6=0.728, P=0.041; within litters: Spearman rank correlation: r_s=0.318, P=0.046), but was not related to number of feeds received per hour of social foraging (between litters: Pearson correlation: r_6=0.196, P=0.642; within litters: Spearman rank correlation: r_s=0.013, N=40, P=0.937).

3.5 DISCUSSION

Social play and aggression were largely unrelated in infant meerkats, and none of the predictions generated by the hypothesis that social play functions to reduce aggression were met.

Rates of play and aggression were not negatively correlated, as predicted by the hypothesis, and the likelihood of foraging encounters ending in strong aggression was unrelated to how frequently pups or litters played. A negative relationship might have been anticipated (at least between litters) because of variations in food availability. Nutritional status positively influences rate of play in meerkats (Chapter 2) and food availability might also be expected to affect the level of competition between pups and thus rates of aggression during social foraging. However, this was not the case, and although the number of potential feeders per pup had a significant effect on hourly rates of encounters and aggression (Table 3.2), the actual amount of food that the pups ate (measured either as number of prey items received per hour of social foraging or as weight gain over the 6-week social foraging period) was not correlated with aggression. This suggests that the pups were competing primarily for access to adults, rather than for food per se.

The distribution of play and aggression during development did not exhibit the negative relationship predicted by the hypothesis. Although rate of play did increase over the social foraging period, concurrent with a decrease in hourly rates of aggression (Fig. 3.1), there was no change in the proportion of encounters that ended in strong aggression. Pups were just as likely to behave aggressively whenever they met throughout the period. The reduction in hourly rates of aggression was caused solely by a decrease in the number of encounters individuals experienced, and this was the result of the pups spacing themselves across the group more evenly during the latter half of the social foraging period (2001).

Similarly, if the primary function of play was to ameliorate potentially harmful aggression between littermates, as suggested from studies on other small carnivores (West 1974; Poole 1978; Soderquist & Serena 2000), we would expect the frequency of play to fall markedly when the meerkats stopped actively competing for food at around 10-12 weeks of age. However, rate of play was unrelated to the pups' foraging status, with play remaining relatively constant even once the youngsters were foraging completely independently (16-26 weeks of age; Fig. 3.1). Of course, littermates do not normally disperse before 18 months of age (Chapter 5), so the opportunity for aggression remains (even though individuals are not competing for food; Barnard 2000), and this potentially explains the persistence of play.

However, rate of play in meerkats falls steadily after 7 months of age (at 12 months they play only one-tenth as frequently as at 3 months; Fig. 6.1), even though littermates are still living together.

The finding that pups that played together frequently behaved just as aggressively toward one another as pups that played together rarely, is strong evidence against the hypothesis. In fact, dyads that shared in play the most, were more likely to indulge in fighting (physical contact with biting) than were any other dyads. This is the reverse of the result anticipated if play served to increase social harmony.

The final prediction generated by the hypothesis, that sharing in play should reduce the subsequent likelihood of interacting with aggression, was also not met. Pups that had played together were just as likely to attack one another during subsequent social foraging encounters (occurring within 10 minutes) as were pups that had not shared a play bout. Although laboratory studies have shown that rats find play pleasurable (Humphreys & Einon 1981), it is unknown whether this 'pleasure' translates into lowered stress levels and a reduced propensity for aggression. Social grooming lowers heart rate in horses, *Equus caballus* (Fey & de Mazieres 1993), and increase levels of beta-endorphins in talapoin monkeys, *Miopithecus talapoin* (Keverne et al. 1989), but it is unknown whether social play has similar physiological effects. The absence of an immediate behavioral effect of play upon aggression in young meerkats suggests that it does not.

The negative findings of this study could potentially be caused by an erroneous acceptance of the null hypothesis (that play and aggression were not related) because of small sample sizes. However, in a power analysis (Thomas & Juanes 1996) of the main results, the statistical tests in which I used individual data (standardized for litter) or dyad data, and the test for the aftereffects of play, were sufficiently powerful to reject the null hypothesis correctly if a biologically meaningful effect had occurred (i.e. if play had accounted for 20% of the variability observed in social foraging aggression). Although it could be argued that the dyad data involved psuedoreplication, because each pup was represented in more than one dyad, it was the relationship between the two pups (each of which was unique) that formed the sample points for this test, not the individuals themselves. In contrast, the tests that used litter data (including the repeated measures ANOVA) were relatively weak statistically and, if not for the corroboratory findings from the other tests, I would view these results with caution.

Although play did not affect aggression in meerkats, aggression did inhibit play. Social foraging pups that had interacted with strong aggression were 40% less likely to play together during the following 10 minutes than pups that had encountered one another without aggression (Fig. 3.2). This result is consistent with anecdotal observations that aggressive interactions inhibit play in primates (Meier & Devanney 1974; Symons 1978b; Stevenson & Poole 1982) and rodents (Taylor 1980; Thompson 1998). It could, however, be argued that relaxed pups (e.g. those not hungry) would be more likely both to meet each other amicably and to indulge in play, in contrast to stressed or hungry pups that would behave more aggressively to competitors and be disinterested in play. However, the original finding, that pups that had just played together were as likely as nonplayers to behave aggressively, shows that there is no inherent coupling between play and nonaggressive foraging encounters, as would be expected if a third variable, such as level of hunger, was creating the relationship.

Aggression also altered the structure of social play in young meerkats, with frequent attacks during foraging inhibiting a pup's tendency to play wrestle (Fig. 3.3). It is unlikely that this negative correlation between play wrestling and aggression was because wrestling reduced the aggressiveness that an individual felt for its wrestling partner, since wrestling showed no relationship with the frequency of launching aggressive attacks. A third variable, such as relative size, could have generated the relationship, because pups that were smaller than their siblings were more prone to attack during social foraging (L. Sharpe unpublished data); however, there was no relationship between relative weight and the likelihood of wrestling during play. In conclusion, it appears likely that frequent attack during foraging actively inhibited play wrestling, even though it did not affect involvement in less intimidating elements of social play, such as mounting, grappling or chasing. This conclusion is consistent with Biben's (1998) finding that squirrel monkeys, *Saimiri sciureus*, that were likely to lose a play fight, were less likely than probable winners to engage in 'directional' wrestling (where one animal pinned the other down) and more likely to initiate 'nondirectional' wrestling bouts (wrestling while hanging from a tree, where win/lose roles were minimized).

Although the finding that aggression inhibits play is intuitively unsurprising, it may have far-reaching implications. We already know that play is highly sensitive to perturbations in the physical environment (Geist 1971; Baldwin & Baldwin 1976; Berger 1980; Lee 1984; Barrett et al. 1992; Sommer & Mendoza-Granados 1995, Chapter 2) and if play is equally sensitive to the social environment, then the risks of aggression inherent in adulthood (i.e. competing for mates, dominance status, territory or resources) could restrict play to the juvenile period in many species (Fagen 1981). This hypothesis contrasts sharply with the traditional perception that the juvenile period provides the optimum window for the accrual of the benefits of play (see Byers & Walker 1995), a perception that has spawned numerous hypotheses of function (Fagen 1976; Smith 1982; Barber 1991; Byers 1998) and has long influenced the direction of our unsuccessful search (Caro 1988; Barber 1991; Spinka 2001) for the adaptive significance of play.

In conclusion, the behaviour of young meerkats provides no evidence to support the hypothesis that social play reduces aggression or increases social harmony. Although it is perilous to extrapolate too widely from the study of a single species, these results cast doubt upon a whole stable of hypotheses that suggest play facilitates social bonding, group cohesion, or alliance formation.

CHAPTER FOUR

FREQUENCY OF SOCIAL PLAY DOES NOT AFFECT DISPERSAL PARTNERSHIPS IN WILD MEERKATS

(*Animal Behaviour*, in press)

4.1 ABSTRACT

The adaptive significance of play is one of ethology's greatest enigmas, yet few of the many hypotheses advanced to explain play, have ever been tested. This study evaluated an aspect of the social bonding hypothesis, which proposes that social play strengthens long-term bonds between individuals, enhancing future alliances. Using data from a wild population, I tested five predictions arising from the hypothesis that meerkats, *Suricata suricatta*, use play to strengthen ties with potential dispersal partners. I found that meerkats did not favour play with the most appropriate potential partners – i.e. they did not prefer their own sex (although they disperse with animals of the same sex only) nor strive to play with younger animals (that they could dominate in a future group) or avoid playing with older animals (that they could not). Frequency of play was unrelated to the size of subsequent dispersal parties, or the likelihood of males undertaking prospecting forays with companions, and preferred playmates were not favored as prospecting partners. Although meerkats preferred to disperse with littermates (and littermates were strongly favored in play), they played no more frequently with their future dispersal partners than with matched controls with whom they did not disperse. I conclude that the strengthening of long-term bonds between potential dispersal partners is not the function of social play in meerkats.

4.2 INTRODUCTION

Despite more than 30 years of research, the adaptive significance of play remains one of ethology's greatest enigmas. Numerous hypotheses have been advanced to elucidate play's function (see Smith 1982; Martin & Caro 1985; Bekoff & Byers 1998; Section 1.3) with potential benefits ranging from the physiological, such as increased cardio-vascular fitness (Gormendio 1988), the modification of synapse distribution in the cerebellum (Byers & Walker 1995), energy regulation (Barber 1991) or the enhancement of cerebral cortex growth (Ferchmin & Eterovic 1979), to the development of skills, such as motor skills (Caro 1988), social skills (Bekoff 1978) or the ability to cope with stressful situations (Spinka et. al. 2001), solve problems (Fagen 1981) or assess risk (Thompson 1998). An alternative hypothesis, that of social bonding, is based on the premise that play acts as an affiliative mechanism, strengthening bonds between play partners, presumably through the provision of strong positive social conditioning (Baldwin 1982). The social bonding hypothesis proposes that play functions to increase social harmony (Drea et al. 1996), reduce dangerous aggression between littermates or group members (Pellis & Pellis 1992; Soderquist & Serena 2000), strengthen an individual's ties to its social group and improve social cohesion (Bekoff 1977b) or enhance long-term alliances between individuals (Berman 1982).

Despite the popularity of the social bonding hypothesis (Baldwin & Baldwin 1974; Bekoff 1974, 1977a,b; Poirier & Smith 1974; Panskepp 1981; Lee 1983; Drea et al. 1996), there is currently little quantitative evidence to either support or refute the tenet that play acts as an affiliative mechanism. Frequency of play is unrelated to frequency of aggression in meerkat pups, *Suricata suricatta* (Chapter 3), and captive red-necked wallabies, *Macropus rufogriseus banksianus* (Watson 1993) and is also unrelated to frequency of affiliative social interactions (i.e. social grooming) in subadult meerkats (Chapter 5). Similarly, sharing in play has no immediate short-term effect on the likelihood of meerkat dyads fighting over food (Chapter 3). However, rate of play increases concurrently with a fall in sibling aggression during the development of captive spotted hyenas, *Crocuta crocuta* (Drea et al. 1996). In captive golden-mantled ground squirrels, *Spermophilus literalis*, littermates, which play more frequently than nonlittermates, also exhibit less agonism (Holmes 1995), and spring-born male voles, *Microtus agrestis*, which play extensively, remain tolerant of male conspecifics, while autumn-born males, which do not play, become aggressive at sexual maturity (Wilson 1973).

The suggestion that play strengthens an individual's ties to its social group, encouraging it to delay dispersal (Bekoff 1977b; Gaines & McClenaghan 1980) is not supported by the available evidence. Although there is some evidence that involvement in non-agonistic social interactions, such as allogrooming, may influence an individual's decision to disperse (Harcourt & Stewart 1981; Harris & White 1992), frequency of social play is unrelated to dispersal behaviour in both meerkats (Chapter 5) and Belding's ground squirrels, *Spermophilus beldingi* (Nunes et al. 2004), in the only studies that have addressed this question.

This study focuses on the final aspect of the social bonding hypothesis, namely that play functions to strengthen long-term alliances between individuals that need to cooperate in the future, such as those that disperse together (Berman 1982; Smith 1982). Unfortunately, the only evidence available to support the hypothesis is anecdotal. Sugiyama (1976), for example, observed 'a few instances' of playmates dispersing together in Japanese monkeys, *Macaca fuscata*, and several studies have found that young male rhesus monkeys, *Macaca mulatta,* transferring into new groups, initially establish relationships with males they knew (and hence played with) in their natal group (Boelkins & Wilson 1972; Hausfater 1972). This study tests the social bonding hypothesis by examining the relationship between social play and dispersal partnerships in a wild population of meerkats, *Suricata suricatta*.

Meerkats are highly gregarious, cooperatively breeding mongooses that live in close-knit groups (of 3-40 individuals) normally comprised of a dominant breeding pair (responsible for 75% of the group's pups; Griffin et al. 2003), the pair's offspring and several immigrant males (Clutton-Brock et al. 2001a). Young meerkats attain sexual maturity at 7-11 months of age and disperse from their natal group at around 18-30 months of age (Clutton-Brock et al. 1998, 2002). Females are aggressively expelled from the group by the dominant female and often suffer several short-term evictions before emigrating (Clutton-Brock et al. 1998, 2001b). Males disperse voluntarily after undertaking repeated short-term prospecting forays to neighbouring groups (ranging in duration from 1-90 days) from around 11 months of age (Doolan & MacDonald 1996; Young 2003).

Meerkats of both sexes normally disperse with same-sexed group members, and the well being of dispersing animals is positively correlated with the number of animals in their party (e.g. large parties enjoy greater foraging efficiency, lighter parasite loads and lower adrenal activity; Young 2003). Dispersing individuals found new groups with opposite-sexed dispersers from other groups, and males may also take over or join established groups (Doolan & MacDonald 1996; Young 2003). In such cases, large coalitions of males are more successful at both seizing and defending dominance in a group (Young 2003). Even in well-established groups, group size is positively related to individual survival and growth rate, female fecundity (Clutton-Brock et al.1999a, 2001a & b; Russell et al. 2002, 2003) and long-term survival of the group (Clutton-Brock et al. 1999a, 1999b; Courchamp et al. 1999).

Evidently, a dispersing meerkat enjoys considerable advantages if other group members are willing to accompany it. If social play is capable of strengthening long-term bonds between individuals, meerkats should use play to nurture ties with suitable dispersal partners, and one would predict: (1) individuals should favour play with animals of the same sex, because they disperse with same-sexed group members only; (2) individuals should attempt to play with younger (smaller) same-sexed group members, and avoid playing with older (larger) same-sexed group members (because it is to an individual's benefit to disperse with partners it can dominate, thus ensuring it gains the dominant position in any future group); (3) individuals that play infrequently should be more likely to disperse, or undertake prospecting forays, alone, because they will be less closely 'bonded'; (5) males should undertake prospecting forays with their preferred play partners; and, most importantly, (6) individuals should disperse with their preferred play partners.

4.3 METHODS

4.3.1 Study population

I carried out the study, between August 1999 and December 2002, working on a natural population of meerkats living on ranchland in the southern Kalahari Desert, 30 km west of Van Zylsrus, South Africa (26°58'S, 21°49'E). See Section 1.6 for details of the study site's topography, vegetation and rainfall. The work was carried out under licenses issued by the Northern Cape Conservation Service, South Africa. All meerkats in the study were habituated to close observation (within 1 metre) and handling, and were individually marked with permanent marker pen on the tail, plus a small patch of snipped fur on the body (both applied unobtrusively while the animals were sunning at the burrow). I collected data on 69 individuals (35 females and 34 males) in 14 litters, from seven groups (see Table 4.1 for litter sizes). Four of these litters were comprised of pups borne by more than one female, but the youngsters (within 2 weeks in age) were raised together as a single litter, and were treated as such in the analysis.

All study groups were monitored on at least 3 days per week and, during the breeding season (the period when prospecting, evictions and dispersal occurred; Young 2003), groups were usually visited twice every day, with approximately 5 hours of observation daily. Groups were monitored until the study individuals either left their natal group permanently (i.e. did not return within 18 months) or attained at least 3 years of age. Eleven study animals (from five litters) died prior to reaching dispersal age (i.e. the age at which a same-sexed littermate first dispersed; Table 4.1), and of the remaining 58, 52 emigrated from their natal group during the course of the study. All dispersing individuals (29 males, 23 females) were observed after they left their natal group and range, and most were followed until they established, or joined, another group. Dispersal partners were observed together on at least three separate occasions after they had emigrated (and were never observed apart), and the majority of partners were observed to remain together for at least 3 months.

Table 4.1. Data collected from the 14 study litters.

litter	litter size at 4 weeks	litter size at adulthood	no. males in litter at adulthood	play partner data	rate of play data
VD9904	5	5	4	p j s	p j s
VE0001/3	9	9	4	p j s	p j s
VF9907	6	4	2	p j s	p j s
VL9903	6	5	2	p j s	p j s
VV0003	4	4	2	p j s	p j s
VW9905	3	3	2	p j s	p j s
VW9906	4	4	3	p j s	p j s
VD9905	5	3	1	p j s	
VV0004/5	7	6	2	j s	j
VY9907/8	5	0	0	p	p
VY0002/3	3	3	2	p	p
VE0004	4	4	3	j	j
VY0007	4	4	3	j	j
VL0002	4	4	2	s	

Age of litter when data was collected: p = pup, j = juvenile, s = subadult.

4.3.2 General analysis

Throughout the analysis I used the following age categories: 'pup' less than 3 months old; 'juvenile' 3-6 months old; 'subadult' 6-12 months old (where sufficient data existed this category was sub-divided into 'subadult 1' 6-9 months and 'subadult 2' 9-12 months); and 'adult' over 12 months old. In all calculations of group size, or the age/sex composition of a group, I adjusted for any temporary absences of group members. Throughout the analysis I have used 'deviation from litter mean' to standardize individual data derived from different litters. I obtained this measure by dividing the value for each individual by the mean value for its litter (hence a value of one equals the mean). I chose this method because it corrects for factors that affect the mean (e.g. litter size, group size and composition, territory quality, season) but maintains interlitter differences in variance (Sokal & Rohlf 1981) that are caused primarily by individual differences between littermates. All references to 'relative' values or rates refer to deviations from the litter mean.

I used parametric statistical tests throughout the analysis except where the data differed significantly from a normal distribution (based on the Kolmogorov-Smirnov test for normality). In these cases, I used equivalent nonparametric tests. All statistical tests were two-tailed, with a significance threshold of 0.05. Means are given +/- SE.

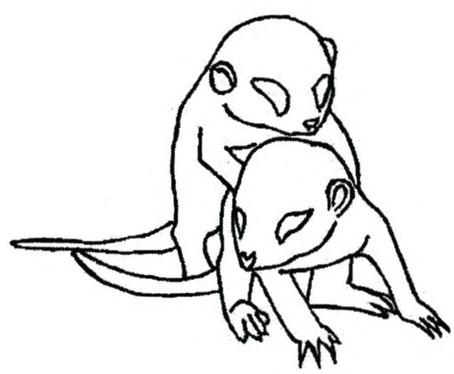
4.3.3 Play partners

Social play in meerkats consists of 'rough and tumble' play, normally referred to as play fighting (Biben 1998). A detailed ethogram of meerkat social play can be found in Wemmer & Flemming 1974, and the age distribution of play in meerkats is presented in Fig 6.1. The most prominent motor patterns adopted by meerkats during play are: pawing - a foreleg is extended toward a companion; biting - inhibited bites are directed toward a companion's head or neck (53%), trunk (18%), legs (17%), or tail (13%; Wemmer & Flemming 1974); wrestling - one animal adopts a submissive posture lying on its back while the other stands on or over it (observed during 39% of play bouts; Fig. 4.1a); mounting - one animal supports its fore body on its companion's back while clasping the other's sides, between the ribcage and groin (observed during 31% of bouts; Fig. 4.1b); grappling - both animals stand bipedally, clasping each other with their forelegs and attempting to push one another over (observed during 14% of bouts; Fig. 4.1c) and chasing/fleeing (25% of bouts).

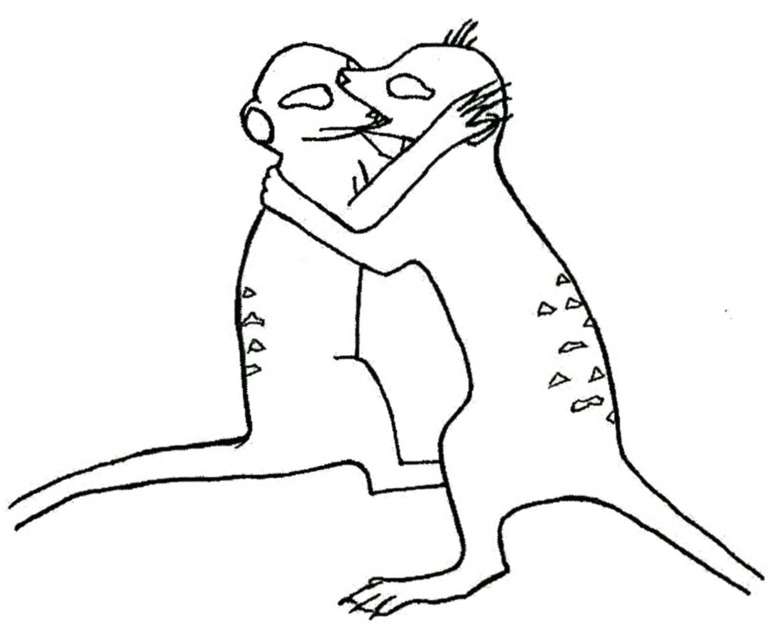
Figure 4.1. Motor patterns frequently observed during social play in meerkats: (a) juveniles wrestling, (b) pups mounting and (c) subadults grappling.

(a)

(b)



(c)



I documented play fights ad libitum (Altmann 1974) whenever a study individual was observed to play with another meerkat. Individual bouts of social play were generally very short and I considered a bout concluded if the pair stopped playing for more than 5 seconds. I recorded the identity of the play partners as a dyad, plus the identity of the initiator of the bout when this was clear (31% of bouts), the presence or absence of 'chatter' calls (a vocalization given by individuals wishing to terminate a social interaction; Manser 1998) and any refusals of play initiations. I collected these data for eight of the study litters throughout their first 12 months of life (beginning at 1 month), and for two additional litters as pups, three as juveniles and two as subadults (Table 4.1). In total, I documented 28,634 play bouts. Play in meerkats over 12 months of age occurred infrequently (with adults devoting only 0.3% of their time to play; Chapter 2), so it was not feasible to record play behaviour for this age group.

To test whether animals preferred to play with same-sexed littermates, I limited the analysis to play bouts shared by littermates. I determined the proportion of each study animal's play bouts it shared with opposite-sexed littermates and the proportion shared with same-sexed littermates. I then calculated the proportions expected by chance (correcting for differences in the amount each littermate played) using the following formula:

$Ab = Pb/Pc$

where Pb was the sum of all bouts undertaken by all potential partners of sex b, Pc was the sum of all bouts undertaken by all potential partners regardless of sex, and Ab was the expected proportion of play bouts that study animal A would share with littermates of sex b. For each study animal, I divided the actual proportion devoted to same-sexed and opposite-sexed partners by their respective expected proportions to produce 'deviation from expected' index values (1=expected, <1=less often than expected, >1 more often than expected). I then averaged these for all members of the litter to produce litter means, and tested whether there was a significant difference between the mean index values for same-sexed partners and opposite-sexed partners using a non-paired *t*-test. Four study litters had to be excluded from the analysis of subadult 2 sex preferences due to an inadequate number of play bouts.

When analyzing play partner preferences between animals of different age, I included play bouts between study animals and nonlittermates only. For each study animal, for each age class, I calculated the percentage of its play bouts that it devoted to each age/sex class present in its group. I then compared these proportions with those expected by chance, given the number of group members in each age/sex class, after correcting for the relative playfulness of each age/sex class, and the relative tendency for the class to play with nonlittermates. I made these two corrections using the following formula:

$$xZ = \frac{((rZ)*(pZ/100))}{((rF)*(pF/100))}$$

where xZ was the relative availability (as a play partner) of an individual in age/sex class Z, expressed in units equivalent to one adult female. rZ was the mean rate of play (measured by one/zero scan sampling) shown by animals of class Z's age and sex; pZ was the mean percentage of play bouts that were normally devoted to nonlittermates by animals of class Z's age and sex; rF was the mean rate of play shown by adult females; and pF was the mean percentage of play bouts devoted to nonlittermates by adult females. For example, the x value (availability as a play partner) of one juvenile male, was 4.9 (equivalent to 4.9 adult females) because, although these young males played 14 times more frequently than adult females, they devoted only 29% of their play interactions to nonlittermates.

When analyzing initiations and refusals of play interactions between animals of different age, I limited the analysis to interactions in which the initiator was known. The resultant sample (2,639 play bouts) was insufficient to examine individual preferences, so I pooled the bouts of all study animals, classifying them on the basis of the sex and age class of the interactants. This resulted in eight categories of same (or mixed) sexed, disparate-aged dyad (mean 165 +/- 29 bouts per category).

4.3.4 Frequency of play

Because play behaviour in meerkats is highly sporadic and relatively rare (occupying around 3% of a youngster's day; Chapter 2), it was not feasible to use conventional sampling methodologies to document individual variation in rate of play (see Section 3.3.3 for more details). I therefore chose one/zero scan sampling (Martin & Bateson 1986) to document frequency of social play. Using a sample interval of 20 seconds (i.e. every 20 seconds I recorded whether each member of the study litter had play fought during the preceding 20 seconds), I began sampling the litter when it emerged from its sleeping burrow around sunrise, and stopped when the group set off to forage, usually 15-90 minutes (mean 37 minutes) later. I targeted this period at the burrow because it is the time at which meerkats play most reliably. Although I refer to the percentage of one/zero scan intervals in which an individual played as its 'rate' of play, one/zero sampling does not provide a true measure of frequency. Nevertheless, the relative rates of play fighting obtained using one/zero sampling were strongly correlated with those obtained using both instantaneous scan sampling (in a subset of seven litters; Chapter 6) and adlib sampling (i.e. number of play bouts; Chapter 10).

For seven study litters, I collected one/zero scan data regularly from 1-12 months of age, obtaining at least four mornings of data on each individual per month (mean 4.8 +/- 0.1). I also collected these data for two additional litters of pups and three litters of juveniles (Table 4.1), obtaining a total of 465 mornings of one/zero scan sampling data. For each age category, I averaged daily rates of play for each study individual, and obtained mean rates for the litter by averaging the rates of individual litter members.

4.3.5 Prospecting forays

Thirty-two male study animals survived to adulthood, and all undertook prospecting forays during the course of the study. Males were identified as prospecting either by their absence from their natal group or by being observed as they approached a neighbouring group. The vast majority of forays lasted only a single day (with males returning in the evening to sleep with their natal group) but occasionally males would be absent for up to 1-2 weeks. In the analysis, I included all forays undertaken between the date of the first foray by a member of the study litter, and the date on which the first male member of the study litter dispersed. This resulted in a sample of 398 prospecting forays by study individuals (mean 12 +/- 2 per individual). I used the number of times a male left its group as the measure of prospecting frequency, and, because females do not prospect, employed 'deviation from the litter's *male* mean' in all analyses, excluding the one study litter that contained only a single male member.

In the analysis of prospecting partner preferences, I assumed that male group members that left their group on the same day were prospecting together, as confirmed by observations of males approaching neighbouring groups (Young 2003). When assessing preferences among male littermates, I excluded litters with fewer than three male members, resulting in a sample of 21 male-male dyads (made up of 17 males from five litters). While it could be argued that the use of dyads resulted in pseudoreplication (as each individual was represented in more than one dyad), the data comprised unrepeated *relationships* between individuals, not repeated individuals per se. For each dyad within a litter, I calculated the proportion of their forays that the two animals shared together (correcting for individual differences in frequency of prospecting), and divided this by the mean proportion recorded for all male-male dyads within the litter. I used the following formula to do this:

$Dxy = Fxy/((Fx+Fy)/2)$

where Fxy was the number of forays that dyad x y undertook together, Fx was the total number of forays recorded for male x, Fy was the total number of forays recorded for male y, and thus Dxy was the proportion of their prospecting forays that dyad xy shared. I also used the above formula to correct for differences in prospecting rate when assessing a study litter's preference for males from different age classes. In this case, x represented the study litter, y represented all members of the specified age class, and F was the number of prospecting *events* (i.e. days upon which one or more members of the age class (or litter) went prospecting). To document the level of preference a litter showed toward its littermates, I calculated a Dxy value for each individual litter member (using prospecting events, and defining y as all *other* members of the litter), and then averaged these individual values to obtain a mean for the litter.

4.4 RESULTS

4.4.1 Play partner preferences

Littermates were strongly favoured as play partners at all ages. Pups rarely played with other group members, devoting only 13 +/- 2.3% of their play interactions to nonlittermates (N=10 litters). Juveniles shared 72 +/- 3.8% of their play bouts with littermates, although they made up only 21 +/- 3.1% of potential partners (N=11). Similarly, subadults dedicated 56 +/- 5.0% of bouts to littermates, which comprised 19 +/- 3.1% of potential partners (N=10; Fig. 4.2). Subadults were six times more likely to play with a littermate than a nonlittermate (paired t test: t_9=7.13, P<0.001).

Meerkats did not, however, show any preference for same-sexed littermates. Pups, juveniles and subadults aged 6-9 months did not favour either sex, but animals aged 9-12 months shared significantly fewer of their play interactions with same-sexed littermates than opposite-sexed littermates (Fig. 4.3). Females seemed to be responsible for this trend, being 62% more likely to refuse a play invitation from a female littermate than from a male (declining 13% versus 8% of invitations) whereas males declined both sexes equally (refusing 9%). Similarly, the average female of this age gave 'chatter' vocalizations (to bring about termination of the play bout) during 13% of bouts shared with a female littermate compared with only 1% of bouts with a male littermate.

Figure 4.2. Mean percentage of play interactions dedicated to littermates, and littermates as a mean percentage of the group, by age class (paired t test: pups: t_9=23.462, P<0.001; juveniles: t_{10}=17.332, P<0.001; subadults: t_9=12.335, P<0.001). Vertical lines indicate SE.

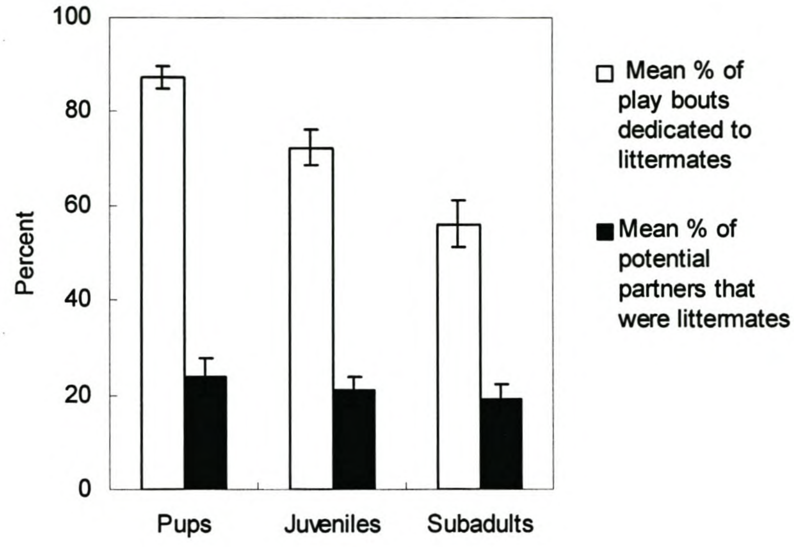
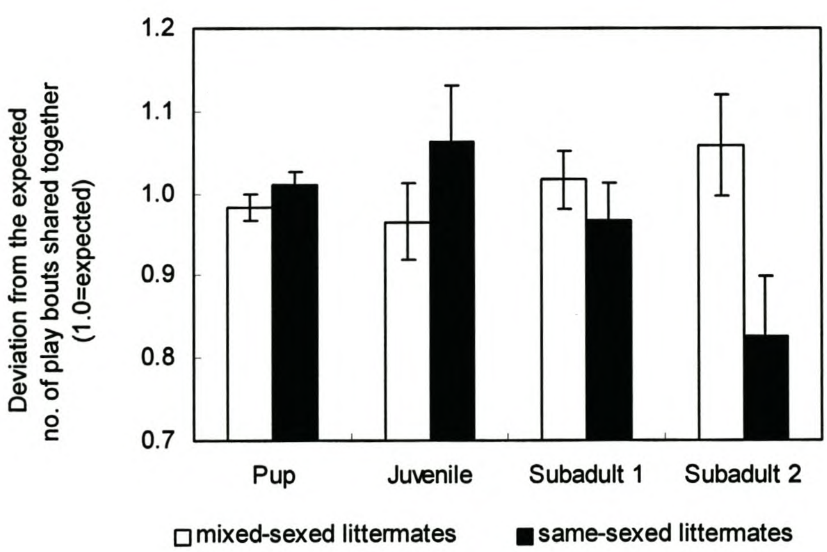


Figure 4.3. Sex preferences among littermates: deviation from the expected number of play bouts shared by mixed-sexed littermates versus same-sexed littermates (t test: pup: t_{18}= -1.301, P=0.21; juvenile: t_{20}= -1.179, P=0.252; subadult 1: t_{16}=0.832, P=0.417; subadult 2: t_{10}=2.407, P=0.037). Vertical lines indicate SE.



Females also showed no preference for their own sex when playing with nonlittermates. Females aged 3-12 months played only half as often as expected with adult females and, as subadults, played less than one-third as often as expected with females 6 months younger than themselves. In contrast, young females consistently played more often than expected with males 3 months their junior (Table 4.2). Male meerkats aged 3-9 months did show a preference for same-sexed group members, playing with males 3 months their elder about 45% more often than expected (Table 4.2). This relationship appeared to be instigated by the younger animal as, in play interactions between males of these age classes, the younger animal refused only 8% of play invitations compared with 35% for the older animal.

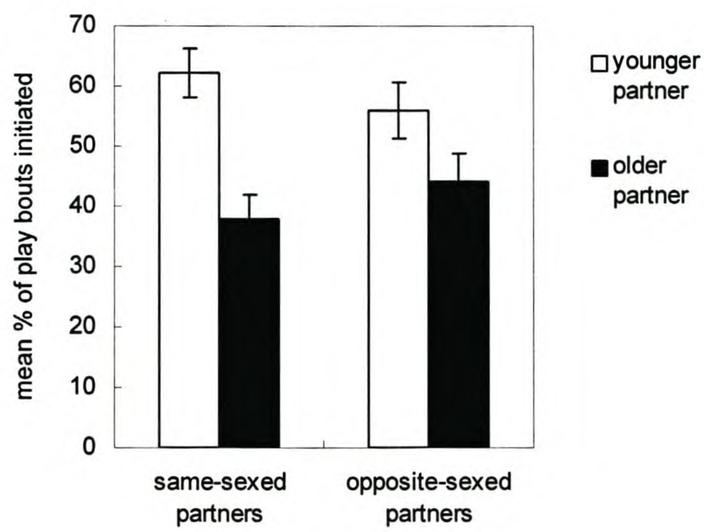
Table 4.2. Significant nonlittermate play partner preferences in meerkats under 1year of age.

Age of study individuals	Female study animals: played more than expected with:	Female study animals: played less than expected with:	Male study animals: played more than expected with:	Male study animals: played less than expected with:
Pup		Adult males W=216.0, N=27, P=0.01 Subadult 2 males W=84, N=14, P=0.005		Adult males t_{22}= -2.457, P=0.022 Subadult 2 males t_{22}= -2.534, P=0.035
Juvenile	Pup males t_{21}= -2.113, P=0.046	Adult females W=322, N=28, P<0.001	Subadult 1 males t_{10}=2.182, P=0.05	Adult males t_{23}= -7.289, P<0.001
Subadult 1	Juvenile males t_{21}=4.216, P<0.001	Adult females W=261, N=26, P<0.001 Pup females W=171, N=18, P<0.001 Pup males W=52, N=11, P=0.019	Subadult 2 males t_{10}=2.261, P=0.045	Juvenile females W=95, N=17, P=0.023 Pup females W=66, N=11, P<0.001 Pup males W=68, N=12, P=0.005
Subadult 2	Subadult 1 males t_{18}=3.384, P=0.003	Adult females W=341, N=27, P<0.001 Juvenile females t_{13}= -4.617, P<0.001		Adult females W=172, N=24, P=0.009

Age/sex classes in which the distribution of play interactions differed significantly from that expected by chance, based on group composition and relative playfulness (see Methods). Paired t tests used except where the data differed significantly from a normal distribution, then Wilcoxon signed-rank test used. (N=individuals).

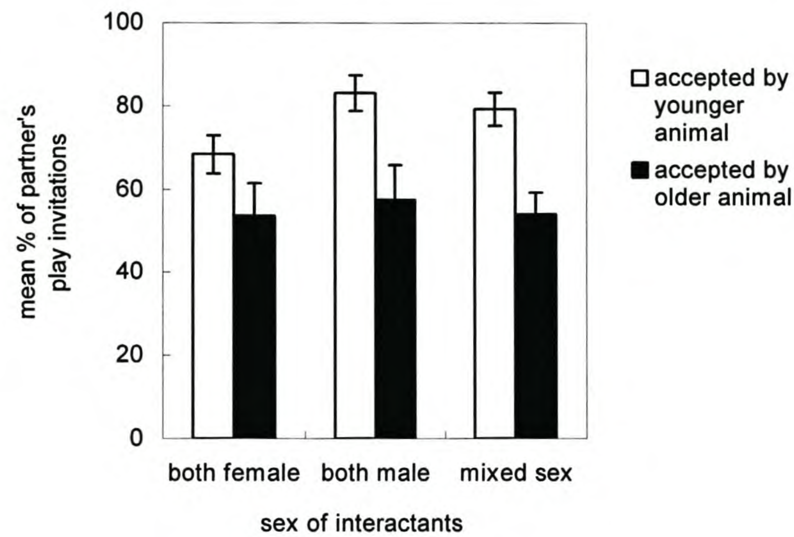
Meerkats did not preferentially try to initiate play with younger same-sexed group members. In fact, the reverse was true: among same-sexed, mixed-aged play partners, the younger animal initiated significantly more interactions (62%) than the older animal (Fig. 4.4). Both males and females behaved in this way, but the trend was only statistically significant for males (paired *t* test: males: t_7=4.466, P=0.003; females: t_7=1.976, P=0.089). Mixed-sexed play partners also showed the same trend with younger animals initiating 56% of bouts (Fig. 4.4).

Figure 4.4. Play interactions between animals of different age: mean percentage of bouts initiated by each partner (paired *t* test: same-sexed: t_7=3.078, P=0.018; mixed-sexed: t_7=2.071, P=0.077). Vertical lines indicate SE.



Meerkats were also almost twice as likely to refuse a play invitation offered by a younger group member than one offered by an older animal. Among males, 43% of play invitations made by younger males were declined, compared with only 17% of invitations from older males (Fig. 4.5). Females also showed this preference for older same-sexed play partners, declining 46% of play invitations from younger females and 32% from older females (Fig. 4.5). Animals playing with opposite-sexed partners refused 45% of invitations from younger animals compared with 21% from older (Fig. 4.5).

Figure 4.5. Play invitations between animals of different age: mean percentage accepted, by age and sex of interactants (paired *t* test: female/female: t_7= -3.305, P=0.013; male/male: t_7= -2.476, P=0.042; mixed sex: t_7= -4.914, P=0.002). Young females accepted fewer invitations from same-sexed partners than did young males (t_7= -3.077, P=0.018). Vertical lines indicate SE.



4.4.2 Prospecting partners

There was no statistical correlation between the proportion of a male's prospecting forays it undertook alone (mean 14.7 +/-2.7%, N=32) and its relative rate of play as a pup or subadult, but there was a positive correlation with play as a juvenile (Spearman rank correlation: pup: r_s=0.143, N=21, P=0.531; juvenile: r_s=0.594, N=27, P=0.001; subadult: r_s=0.197, N=19, P=0.414). There was also no correlation between the relative number of play bouts a male devoted to older male group members prior to adulthood and the relative proportion of his prospecting forays that he shared with older males (r_s=0.057, N=31, P=0.759).

When prospecting, males showed no particular preference for littermates, despite strongly favouring them during play. On average, study males shared 42% of their prospecting forays with littermates, compared with 44% shared with males 3 months older than themselves, and 64% with males 6-12 months their senior (paired *t* test: 3 months older: t_6=0.112, P=0.915; 6-12mths older: t_{11}= -1.326, P=0.133). Study males also showed no preference for males 3 months their elder, as compared with males 6-12 months older (paired *t* test: t_7= -1.567,

P=0.161) despite favouring the former age group during play. In fact, males 3 months older than the study litter were accompanied by study animals on 39% of their own forays, compared with 37% for males 6-12mths older (paired t test: t_7=0.767, P=0.468), indicating that the study animals were accompanying other group members in proportion to their availability (the value for littermates was 42%) and were not differentiating between potential partners on the basis of age. Among male littermates, there was no correlation between a dyad's tendency to go on prospecting forays together and the number of play bouts the dyad shared together prior to adulthood (both variables measured relative to the litter's mean male/male dyad; r_{19}=0.292, P=0.199).

4.4.3 Dispersal partners

Fifty-two study animals dispersed during the study, and none dispersed alone. As anticipated, meerkats did prefer to disperse with littermates rather than older or younger group members (X^2=6.364, P=0.042). Of the 44 dispersing study individuals that possessed same-sexed littermates, 75% dispersed in the company of a littermate. In comparison, of the 46 dispersing study animals that had older same-sexed siblings that were also emigrating at the time, only 54% dispersed with one of these older group members. Similarly, of the 49 dispersing animals that had younger same-sexed group members outside their group at the time of dispersal (evicted or prospecting), 51% dispersed with a younger sibling (Fig. 4.6).

There was no relationship between the mean size of male dispersal parties (6.5 +/- 1.4 individuals, N=13) and mean frequency of play, at any age, when litters were compared (Spearman rank correlation: pup: r_s=0.097, N=8, P=0.794; juvenile: r_s=0.404, N=10, P=0.227; subadult: r_s=0.655, N=7, P=0.096). The mean size of female dispersal parties (3.4 +/- 0.4 individuals, N=12) was also not related to mean rate of play in pups or juveniles, but showed a negative correlation with play as a subadult (Pearson correlation: pup: r_6= -0.212, P=0.614; juvenile: r_7= -0.11, P=0.777; subadult: r_5= -0.793, P=0.033).

Animals that dispersed together were no more likely to have played together as subadults than animals that did not disperse together. In 15 dispersal events (seven involving males and eight females), one or more study animals dispersed in the company of a group member whose same-sexed littermate did not join the dispersal party (although more than half of these control individuals did disperse themselves). There was no significant difference in the mean frequency with which the study individuals played with their dispersal partner as compared with the control (Wilcoxon signed-rank test: W=30.0, N=15, P=0.266; Fig. 4.7). On average, study individuals devoted 4.6 +/- 1.5% of their subadult play interactions to their subsequent dispersal partner compared with 5.1 +/- 1.7% to the control (Fig. 4.7).

Figure 4.6. Percentage of dispersing study animals that chose to disperse in the company of an available older, younger or same-aged group member.

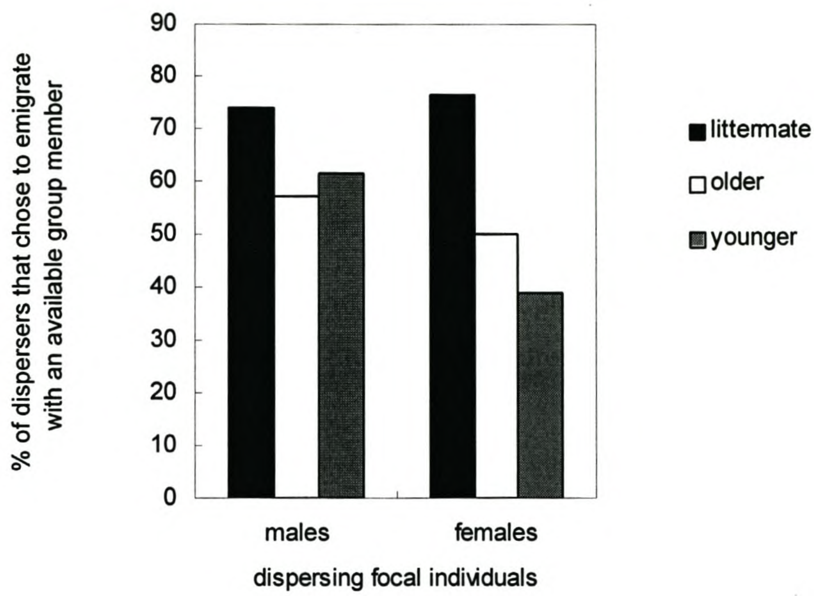
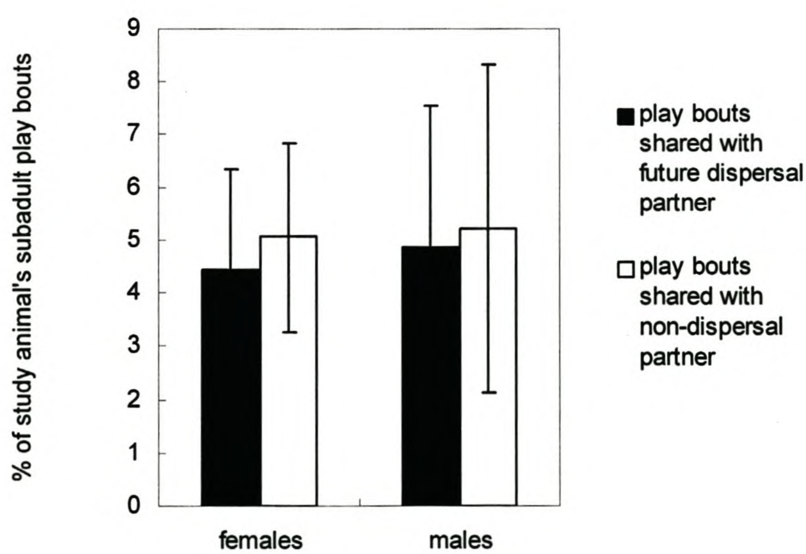


Figure 4.7. Percentage of their play bouts that subadult study animals shared with their future dispersal partner as compared with a matched (same-sexed, same-aged) group member with which they did not disperse, by sex. Vertical lines indicate SE.



4.5 DISCUSSION

The hypothesis that meerkats use social play to strengthen long-term bonds with potential dispersal partners was not supported by the findings of this study. Although meerkats disperse with same-sexed group members only, they showed little preference for their own sex during play. Despite strongly favouring play with littermates (Fig. 4.2), meerkats did not prefer littermates of the same sex (Fig. 4.3), in fact, females over 9 months of age actively avoided playing with same-sexed peers. Female meerkats also showed no preference for their own sex when playing with nonlittermates, consistently favouring younger brothers, and playing less than expected with adult females. Males, however, favoured their older brothers, and were only half as likely as females to refuse a play invitation offered by an older same-sexed animal (Fig. 4.5). Nevertheless, neither sex favoured play with younger same-sexed group members as predicted by the hypothesis, and the distribution of initiations and refusals makes it clear that younger animals actively sought play with their elders (Figs. 4.3 & 4.4). Although it is possible that age-related differences in rates of play generated this distribution (i.e. younger animals play more frequently so initiate play more often and suffer more refusals), the same age-biased distribution was found in interactions between pups and juveniles, whose rates of play are virtually identical (Chapter 6).

The third prediction of the hypothesis, that individuals that played less frequently should be more likely to disperse alone (because of weaker ties with potential partners), could not be tested, as none of the study animals emigrated alone. However, the frequency with which a litter indulged in social play was not positively related to the mean size of its subsequent dispersal parties, and male dispersal parties were almost twice as large as female parties even though both sexes played at the same rate (Chapter 6). Relative rate of play also had no effect on the likelihood of males prospecting alone.

Male meerkats did not prefer to go prospecting with the males that they played with most frequently (prediction four); in fact, they showed no apparent discrimination between potential prospecting partners, accompanying males of all ages simply in proportion to their availability. Dispersing meerkats, however, were more likely to emigrate with littermates than with other available group members (Fig. 4.6). Since littermates were also strongly favoured in play (Fig. 4.2), this preference was consistent with the final, and most important, of the predictions generated by the social bonding hypothesis. However, individuals played no more frequently with their future dispersal partners than with matched controls with which they did not disperse (Fig. 4.7), clearly demonstrating that social play was not causing the relationship between play and dispersal partnerships among littermates. The meerkats' preference for same-aged dispersal partners was, almost certainly, the manifestation of individuals seeking to avoid older (and larger, since meerkats grow through out their lives; Clutton-Brock et al. 1999a) dispersal partners that would be difficult to defeat in any future contest for dominance.

The negative findings of this study should not be accepted without first considering whether the study's sample sizes were large enough to allow the null hypothesis (i.e. that play behaviour and choice of dispersal partner were unrelated) to be rejected if a biologically meaningful relationship had existed between play and the various outcome variables. Although post-hoc power analyses are sometimes used to assess this question (Thomas & Juanes 1996), the validity of such post-hoc testing is questionable (Hoenig & Heisey 2001) and it may be more valuable to note that the data did not show any trend toward a rejection of the null hypothesis; for example, the sample used to test the most critical of the hypothesis's predictions (that meerkats will disperse with individuals which they played with most often) consisted of 15 dispersal events, and in only three of these events did the study animals play more frequently with their future dispersal partner than with the control.

The finding that frequency of play has no long-term, downstream effect on the formation of dispersal partnerships in this species is consistent with the results of earlier studies. The findings of Chapter 5 revealed that frequency of play was unrelated to the apparent strength of a meerkat's bonds to its social group (measured as duration of tenancy in the group and level of contribution to the group's activities). Similarly, frequency of play was not related to any indicator of social harmony, such as frequency of social grooming (Chapter 5) or aggression (Chapter 3), and sharing in play had no immediate short-term effect on the likelihood of meerkats interacting aggressively (Chapter 3). Taken in conjunction, these results suggest strongly that play does not act as an affiliative mechanism in this species, and that social bonding is neither the primary function, nor a subsidiary benefit, of meerkat play.

Nevertheless, even if meerkat play does not have a demonstrable affiliative effect, it may still influence an individual's choice of dispersal partner. The inherent competitiveness of play fighting (Thompson 1998) could provide a young meerkat with the opportunity to assess the relative skill and abilities of potential dispersal partners. Considering that a dispersing meerkat must weigh the survival benefits gained from emigrating in a large party (Young 2003) against the reproductive cost of increased competition for the lucrative dominant breeding position in their new group, an individual that is able to minimize this cost, by dispersing with animals it can defeat in battle, will enjoy a strong selective advantage.

However, despite this selection pressure, it seems unlikely that the primary function of meerkat play is the assessment of potential partners, because young meerkats devote more than 50% of their play interactions to opposite-sexed animals with which they will never disperse or compete. Even if young meerkats are gleaning information about relative competitive abilities from their play interactions, they do not appear to apply the knowledge in other social contexts. For example, the frequency with which a subadult meerkat wins play fights (i.e. attains the dominant, 'on top' wrestling position; Fig 4.1a) with same-sex littermates is unrelated to its likelihood of initiating agonistic, status-related interactions with these same animals (Chapter 9). Similarly, degree of success during play does not affect the likelihood of a meerkat pup launching an attack on its playmates during competition over food (L. L. Sharpe unpublished data). Even more compelling is the finding that, in subadults, dyads that share a heavily biased play relationship (i.e. one individual wins almost all of the pair's play fights) compete for dominance just as frequently as dyads that are evenly matched in play, and the habitual 'losers' initiate these aggressive interactions as frequently as the 'winners' (Chapter 9).

The finding that young meerkats do not appear to be influenced by the relative play performance of their competitors is perhaps unsurprising because - although play fighting superficially resembles genuine combat – play success is not predictive of victory in serious fights for the dominant position within a group (Chapter 6), and thus information about competitive ability gained through play is unlikely to be reliable. Nevertheless, a meerkat's level of success during play fighting does appear to reflect its social status within the group; for example, among older meerkats, females, which are socially dominant to males, win two-thirds of all mixed-sexed play bouts (Fig. 9.5) even though meerkats are sexually monomorphic (Clutton-Brock et al. 2002) and the sexes play at identical frequencies (Chapter 6). A similar concurrence between play roles and social status has been observed in squirrel monkeys, *Saimiri sciureus* (Biben 1998), male baboons, *Papio anubis* (Owens 1975), male domestic rats, *Rattus norvegicus* (Pellis & Pellis 1992), and red foxes, *Vulpes vulpes* (Myer & Weber 1996), but was not detected in domestic horses, *Equus callabus* (Araba & Cromwell-Davis 1994), red-necked wallabies (Watson 1993), rhesus monkeys (Symons 1978b), or female baboons (Owens 1975). Although some authors have suggested that the function of play is the formation or maintenance of dominance rankings (Carpenter 1934; Poirier & Smith 1974; Paquette 1994; Myer & Weber 1996), rank in meerkats is rarely established among same-aged peers (i.e. primary play and dispersal partners) prior to dispersal from the natal group (Chapter 8). More importantly, as Symons (1978a) argues, play fights could not remain playful if used to establish rank, because individuals would have to react to play initiations as they would to a threat or challenge (i.e. with either submission or escalation).

In conclusion, this study found no evidence to suggest that social play is used by meerkats to establish long-term bonds or alliances with potential dispersal partners.

CHAPTER FIVE

PLAY DOES NOT ENHANCE SOCIAL COHESION IN A COOPERATIVE MAMMAL

(*Animal Behaviour*, in press)

5.1 ABSTRACT

The social cohesion hypothesis of play asserts that the adaptive function of social play is to strengthen affiliative ties between group members, thereby increasing cohesion within the social group. Although this hypothesis is frequently cited, it has never been quantitatively tested. This study uses data collected from a wild population of cooperative mongoose (the meerkat, *Suricata suricatta*) to test four predictions arising from the hypothesis: firstly, that an individual's frequency of play, and mean number of play partners, will be positively correlated with group size (because individuals in large groups must strengthen ties with a greater number of animals); secondly, an individual's frequency of play will be positively related to frequency of other affiliative interactions such as allogrooming; thirdly, an individual's frequency of play will be positively correlated with level of contribution to cooperative group activities (based on the assumption that individuals that are closely bonded to their group will invest more heavily in the group than those with weak ties); and finally, an individual's frequency of play will be positively correlated with duration of tenancy in the natal group. The behaviour of young meerkats failed to fulfill any of these predictions, and I conclude that social play is unlikely to have the capacity to promote social cohesion in mammals.

5.2 INTRODUCTION

'Animals that play together, stay together' (Poirier et al. 1978) is the underlying tenet of the social cohesion hypothesis, one of more than 30 hypotheses (Baldwin & Baldwin 1977) that have been advanced to explain the adaptive significance of play. The social cohesion hypothesis (Bekoff 1977b) asserts that play's primary function is to strengthen affiliative ties between group members, thereby increasing cohesion within the group. While play's influence on social cohesion is often asserted (Jay 1963; Hall 1968; Poirier 1969; Baldwin & Baldwin 1974; Bekoff 1974, 1977a, 1977b, 1982; Poirier & Smith 1974; Poirier et al. 1978; Gaines & McClenaghan 1980; Panskepp 1981; Berman 1982; Lee 1983; Bekoff & Byers 1985; Holmes 1995; Drea et al. 1996), and Bekoff (1977b, 1982) formulated a prediction by which the hypothesis could be tested (i.e. that individual differences in frequency of play will be reflected in differences in age at dispersal), no attempt has been made to quantitatively test the hypothesis.

This study examines the relationship between play and social cohesion in a wild population of social mongoose (the meerkat, *Suricata suricatta),* testing four predictions arising from the hypothesis. The first prediction is that an individual's frequency of social play, and its mean number of play partners, should be positively correlated with group size, because animals living in large groups must strengthen ties with a greater number of partners to prevent group fragmentation. This is particularly relevant to a cooperative species such as the meerkat, in which group size (3-40 individuals) is positively related to survival, growth rate and fecundity (Clutton-Brock et al. 1999a, 2001b, 2001c; Courchamp et al. 1999; Russell et al. 2002, 2003). Secondly, if play functions to promote affiliation between group members, one would expect a positive relationship between an individual's frequency of social play and its involvement in other types of affiliative interaction such as allogrooming.

The third prediction assessed in this study arises from the assumption that individuals that are closely bonded to their social group will invest more heavily in cooperative group activities than individuals whose ties to the group are weak. This is likely to be the case for two reasons: firstly, individuals with strong affectional ties to members of their group may be more inclined to undertake behaviours that directly benefit those animals (e.g. anti-predator behaviour, allogrooming - Seyfarth & Cheney 1984), and, secondly, they will accrue more long-term benefits from their investment in group activities (e.g. the benefits of increased group size as a consequence of helping care for infants; Clutton-Brock et al. 2001c; Young 2003) because they are likely to remain in the group for longer. In meerkats, all members of the group assist in a range of cooperative behaviours such as pup raising (Clutton-Brock et al. 2000, 2001a, 2002; Brotherton et al. 2001) and anti-predator behaviour (Clutton-Brock et al. 1999b), and I predict that an individual's level of contribution to these cooperative activities should be positively correlated with its frequency of play. Finally, I test Bekoff's (1977b, 1982) prediction that intralitter differences in frequency of social play should be positively related to duration of tenancy in the natal group.

5.3 METHODS

5.3.1 Study population

I carried out the study between August 1999 and November 2003, working on a natural population of meerkats living on ranchland in the southern Kalahari Desert, 30 km west of Van Zylsrus, South Africa (26°58'S, 21°49'E). See Section 1.6 for details of the study site's topography, vegetation and rainfall. The work was carried out under licenses issued by the Northern Cape Conservation Service, South Africa.

Meerkats attain sexual maturity at 7-11 months of age, and both sexes disperse from their natal group at 18-30 months of age (Clutton-Brock et al. 1998, 2002). Young females are aggressively evicted by the group's dominant female (when she is in late pregnancy), often with assistance from other group members (Clutton-Brock et al. 1998). Subordinate females frequently suffer several short-term evictions (across a number of the dominant's breeding events) before finally emigrating from the group. In contrast, males appear to disperse voluntarily, after undertaking frequent, short-term prospecting forays to neighbouring groups from around 11 months of age (Doolan & MacDonald 1996; Young 2003).

I collected data on 55 individual meerkats (26 females and 29 males) in 11 litters from seven groups. Three of these study litters were comprised of pups borne by more than one female, but the youngsters (within 2 weeks in age) were always raised together as a single litter, and were treated as such in this analysis. Two female study animals died prior to adulthood and were excluded from all analyses (except that of litter size). All study animals were habituated to close observation and handling, and were individually marked with coloured permanent marker pen on the tail, and a small patch of snipped fur on the body (both applied unobtrusively while the animals were sunning at the burrow). All study animals were monitored several times each week throughout their lives, until they either died (four females), dispersed from their natal group (21 females & 29 males) or attained the dominant position within their natal group (one female). All dispersing animals were observed after they left their natal group and most were followed until they established or joined another group. I used the following age categories: pup - <3 months old; juvenile - 3-6 months old; subadult - 6-12 months old; and adult - >12 months old.

5.3.2 Data collection

I recorded social play (also referred to as play fighting) using two different methods (both described in Section 3.3.3; see also Wemmer & Flemming 1974 for a detailed ethogram of meerkat play). To quantify play partner choice, I recorded play fights ad libitum (Altmann 1974) whenever a study individual was seen to play with another group member. In total, I recorded the identity of participants in 26,217 play fights. I used one/zero scan sampling (Martin & Bateson 1986) to measure frequency of social play in study individuals because the low and sporadic frequency of play in meerkats precluded the use of conventional sampling methodologies (see Section 3.3.3 for further details, plus definitions, exclusions, etc.). I collected one/zero scan data when the group was at their burrow in the morning, and obtained at least four mornings of data on each individual each month (mean 4.8 +/- 0.1), totalling 456 mornings of scan sampling data. I averaged daily rates of play for each study individual to obtain a mean value for each age period. Although I refer to the proportion of scan intervals that included social play as an individual's 'rate' of play, it should be noted that one/zero scan sampling doesn't provide a true measure of frequency. Nevertheless, the relative rate of play obtained using one/zero sampling was significantly correlated with that obtained using instantaneous scan sampling (Altmann 1974) for seven litters of pups that were sampled by both means (Spearman rank correlation: r_s=0.512, N=28, P=0.006).

I used allogrooming interactions to measure the degree of affiliation exhibited by group members, and recorded allogrooming bouts ad libitum (Altmann 1974) whenever I observed a study animal groom, or be groomed by, another meerkat. I documented the identity of the participants, the initiator of the grooming bout and whether the recipient reciprocated. I considered a grooming bout to have concluded when the interactants undertook another behaviour for more than 1 minute. I collected allogrooming records for eight of the study litters when they were aged 3-12 months (2,546 grooming bouts).

To assess contribution to group activities (also referred to as helping behaviour), I used two measures of nonreproductive help: 'burrow maintenance', an individual excavates sand from the group's communal sleeping burrows or from the bolt-holes used in predator escape, and 'sentinel duty', an individual forgoes foraging to watch for predators from an elevated perch; and two measures of pup care: 'babysitting', an individual foregoes foraging to remain at the natal burrow with pups aged less than 28 days, and 'pup-feeding', an individual donates food items to pups aged 1-3 months. See Table 5.1 for details of how each of these measures was quantified.

Since nutritional status was a potential confounding variable in this study, I recorded the body weight (an accurate measure of condition in young meerkats; White 2001) of study animals by enticing them, with a crumb (<0.5g) of hard-boiled egg, to stand on an electronic balance. Animals were generally weighed three times each week, first thing in the morning, before they left the burrow to forage. I averaged an individuals weight measurements on a 2-weekly basis and then averaged these bi-weekly means to produce a value for each age class.

For seven of the study litters (37 individuals) I documented play behaviour and body weight throughout the first 12 months of life (beginning at 1 month of age when the pups started moving with the group). For these litters, contribution to group activities was measured during two periods: subadult and adult (12-18 months of age). I collected supplementary data on four additional litters, recording play behaviour and weight in one litter of pups (three individuals), and in three litters of juveniles (15 individuals). For these supplementary litters, contribution to group activities was documented during the adult period only.

5.3.3. Analysis

Although young meerkats show no sex difference in rate of play (Fig. 6.2), rate of allogrooming (L. L. Sharpe unpublished data), or body weight (White 2001), the sexes do differ in their contribution to cooperative activities (Clutton-Brock et al. 2002) and in the proximate cause of dispersal (as outlined above). As a consequence, for all analyses except the comparison of play and allogrooming, I analysed data for the sexes separately and, when evaluating differences between members of a litter, compared individuals with their same-sexed littermates only. To do this, I converted the data to 'deviations from same-sex litter mean' by dividing the value recorded for each individual by the mean value for all litter members of that sex (hence a value of one equals the litter's mean). Those individuals (five) that were a litter's sole representative of a sex were excluded from these analyses. I chose this method of standardizing the data because it corrects for factors that affect the litter mean (such as group size and composition, territory quality, food availability) but maintains interlitter differences in variance (caused primarily by individual differences between littermates). All references to 'relative' values or rates refer to deviations from same-sex litter mean (or deviations from total litter mean in the case of allogrooming).

When analyzing relative frequency of allogrooming, I used the number of times a study animal was seen to groom another group member (over 3 months of age), regardless of whether the animal initiated the interaction or not. There was, however, a strong correlation between relative rate of grooming others and relative rate of being groomed by others (Spearman rank correlation: r_s=0.91, N=38, P<0.001). Pups were excluded from all analyses of allogrooming because they did not actively participate in this behaviour. For the analysis of grooming partner preferences, I used data collected for subadult study animals only, because juveniles groomed others infrequently. Sample sizes were insufficient (mean 48 +/- 7 bouts per individual) to allow detailed analysis of individual preferences, so I pooled and averaged records for all study animals within a litter, and used the resulting eight litter means throughout the analysis. I compared the proportion of a litter's grooming initiations that was directed toward each age class present in the group (excluding pups) with that expected by chance, based on the number of potential partners (assuming that all group members were equally available as recipients of grooming).

When examining the downstream effect of play on contribution to group activities, I used the measure 'relative play (or relative weight) prior to adulthood'. Since intralitter differences in rate of play (and in body weight) were generally maintained throughout the first 12 months of life (with a strong correlation between age classes for both variables; Pearsons correlation: play: pup/juvenile: r_{30}=0.713, P<0.001; juvenile/subadult: r_{30}=0.476, P=0.006; weight: pup/juvenile: r_{30}=0.936, P<0.001; juvenile/subadult: r_{30}=0.909, P<0.001), I amalgamated the age classes by averaging an individual's relative values (for the seven main study litters). For the supplementary study litters, I used the relative values obtained during the sampled age class only, assuming that this provided an accurate representation of the whole pre-adult period. One supplementary study litter was excluded from this analysis of adult contribution due to the emigration of half its members, and one main study litter was excluded from the analysis of adult babysitting because it's group did not bear pups during the period.

In the analysis of male prospecting behaviour, I used the number of times a male left its natal group as the measure of prospecting frequency, and I included, for each study litter, all forays undertaken between the date of the first foray by a member of the litter, and the date on which the first male member of the litter dispersed. This resulted in a total sample of 379 prospecting forays undertaken by study individuals (mean 13.1 +/- 2.2, N=29). In the analysis of age at dispersal, I excluded from the calculation of same-sex means the four animals (all female) that died prior to the dispersal of at least one same-sexed littermate. I also excluded the one female that inherited the dominant position in her natal group (because she will not disperse).

I used parametric statistical tests throughout the analysis except where the data differed significantly from a normal distribution (based on the Kolmogorov-Smirnov test for normality). In these cases, I used equivalent nonparametric tests. All statistical tests were two-tailed with a significance threshold of 0.05. Means are given +/- SE.

5.4 RESULTS

5.4.1 Group size

There was no correlation between group size (mean 18.0 +/- 1.7, range 10-25, N=11) and mean rate of play in meerkats of any age (Pearson correlation: pup: r_6= -0.278, P=0.505; juvenile: r_8= -0.491, P=0.15; subadult: r_5=0.059, P=0.9). Mean rate of play was also not correlated with litter size (mean 5.0 +/- 0.6, range 3-9, N=11; Pearson correlation: pup: r_6=0.324, P=0.434; juvenile: r_8= -0.206, P=0.567; subadult: r_5= -0.328, P=0.472).

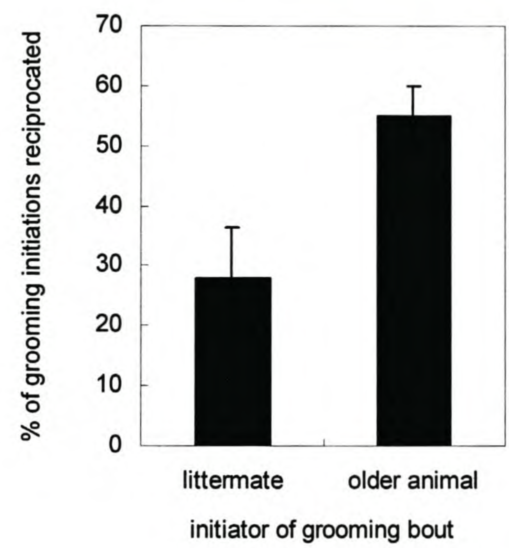
The mean number of partners with which an individual played (i.e. the number of animals with which it shared at least 2% of its play bouts) was also unrelated to the number of animals in its group (Spearman rank correlation: pup: r_s= -0.209, N=9, P=0.55; Pearson correlation: juvenile: r_9= 0.232, P=0.493; subadult: r_8=0.495, P=0.146). On average, pups shared play bouts with 36.5 +/- 3.5% of their group's members, juveniles with 44.2 +/- 4.9% and subadults with 49.7 +/- 3.7%.

5.4.2 Allogrooming

There was no relationship between an individuals' relative rate of play and its relative participation in allogrooming, either for juveniles (Spearman rank correlation: r_s=0.137, N=38, P=0.411) or subadults (Pearson correlation: r_{29}= -0.043, P=0.82). Subadults initiated grooming bouts with littermates significantly less frequently than was expected by chance (paired t test: t_7= -2.501, P=0.041), even though they favoured littermates strongly during play (devoting 56% of play bouts to littermates, which comprised only 19% of their group;

Sharpe in press b). Subadults, however, initiated grooming bouts with older animals significantly more frequently than expected (t_7=3.927, P=0.006) and were twice as likely to reciprocate a grooming bout initiated by an older group member than a bout initiated by a littermate (reciprocating 55.3 +/- 5.8% and 27.6 +/- 8.4% respectively; Fig. 5.1).

Figure 5.1. Mean percentage of social grooming initiations that were reciprocated, by age of initiator (paired t test: t_7=2.795, P=0.031). Vertical lines indicate SE.



5.4.3 Contribution to cooperative activities

In subadult meerkats, there was no correlation between relative rate of play and relative contribution to any cooperative activity (Table 5.1). There was also no downstream effect of play on helping behaviour, with relative rate of play prior to adulthood not correlated with relative contribution to any group activity as an adult (Table 5.1). The same results were obtained when data for the sexes were tested separately.

In subadults, relative contribution to cooperative activities was unrelated to relative body weight, except for contribution to pup-feeding which showed a positive correlation (Table 5.1). Similarly, relative weight during the 11 months preceding adulthood was unrelated to subsequent helping behaviour as an adult, except for an individual's relative contribution to sentinel duty (Table 5.1).

Table 5.1. Correlations between contribution to cooperative activities and rate of play, or body weight.

	Relative contribution to:			
	Pup care		Nonreproductive help	
	Baby-sitting	Pup-feeding	Burrow maintenance	Sentinel duty
Subadults:				
Relative rate of play	r_{30}= -0.025, P=0.894	r_{30}= -0.085, P=0.644	r_{30}=0.127, P=0.488	r_{30}= -0.066, P=0.719
Relative weight	r_{30}=0.016, P=0.932	r_{30}=0.436, P=0.013	r_{30}=0.08, P=0.665	r_{30}=0.467, P=0.007
Adults:				
Relative rate of play prior to adulthood	r_{33}=0.011, P=0.948	r_{39}=0.128, P=0.424	r_{39}= -0.046, P=0.777	r_{39}= -0.171, P=0.284
Relative weight prior to adulthood	r_{33}= -0.035, P=0.84	r_{39}=0.27, P=0.088	r_{39}=0.07, P=0.662	r_{39}=0.356, P=0.022

All variables expressed as deviations from same-sex mean, and Pearson correlation used throughout.

Contribution was measured as follows: babysitting, number of days a individual babysat (mean 6.7 +/- 0.7 per individual, N=53); pup-feeding, number of prey items an individual donated (mean 68 +/- 5 per individual, N=53); burrow maintenance, number of times an individual was observed excavating a burrow (a bout of digging was considered over if the animal moved to a different burrow or stopped excavating for more than 1 minute) (mean 75 +/- 9 bouts per individual, N=53); and sentinel duty, number of times an individual went up on lookout (mean 40 +/- 5 per individual, N=53).

Weight differences between same-sex littermates were not related to relative rates of play, either in subadults (Pearson correlation: r_{30}=0.104, P=0.573) or during the 11 months preceeding adulthood (Pearson correlation: r_{39}=0.271, P=0.087).

5.4.4 Tenancy in natal group

On average, the males in this study dispersed from their natal group at 23.7 +/- 1.6 months of age (N=27) and the females at 24.7 +/- 1.0 months (N=21). When litters were compared, there was no correlation between mean age at dispersal and mean rate of play at any age prior to adulthood, for either males (Pearson correlation: pups: r_6=0.68, P=0.064; juveniles: r_8=0.022, P=0.952; subadults: r_5=0.067, P=0.886) or females (Pearson correlation: pups: r_6=0.136, P=0.748; juveniles: r_8= -0.152, P=0.676; subadults: r_5= -0.316, P=0.49).

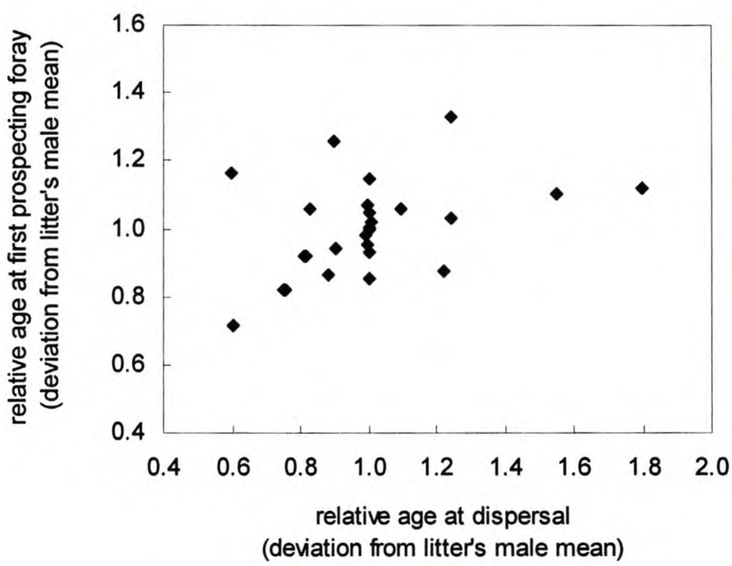
Similarly, animals that played more frequently than their same-sexed littermates spent no longer in their natal group than those that played less frequently. There was no correlation between an individual's age at dispersal and its frequency of play prior to adulthood (both measured relative to same-sexed littermates; Spearman rank correlation: r_s=0.016, N=44, P=0.917). The same result was obtained when data for the sexes were tested separately.

Among females, age at first eviction from the group (mean 21.9 +/- 0.7 months, N=21) was not related to rate of play prior to adulthood (both measured relative to same-sexed littermates; Spearman rank correlation: r_s= -0.368, N=15, P=0.171). Relative age at first eviction, and at dispersal, were also unrelated to the relative amount a female played, prior to adulthood, with her group's dominant female (Spearman rank correlation: eviction: r_s=0.057, N=15, P=0.832; dispersal: r_s=0.096, N=15, P=0.724) or nonlittermates (Spearman rank correlation: eviction: r_s= -0.499, N=15, P=0.056; dispersal: r_s=0.263, N=15, P=0.332). There was also no correlation between relative age at first eviction and age at dispersal (Spearman rank correlation: r_s=0.053, N=15, P=0.842).

Among males, there was no correlation between age at first prospecting foray (mean 11.2 +/- 0.8 months, N=29) and frequency of play prior to adulthood (both measured relative to same-sexed littermates; Pearson correlation: r_{27}=0.135, P=0.485). Similarly, the relative frequency with which males left their natal group to go prospecting showed no correlation with relative rate of play prior to adulthood (Pearson correlation: r_{27}=0.131, P=0.499). However, there was a positive correlation between relative age at first prospecting foray and relative age at dispersal (Spearman rank correlation: r_s=0.449, N=29, P=0.015; Fig. 5.2) even though, on average, males started prospecting 12.5 +/- 1.7 months before they dispersed (*N*=29).

Relative weight prior to adulthood was not related to relative age at first eviction, first prospecting foray or dispersal, for either sex.

Figure 5.2. Relative age at first prospecting foray as a function of relative age at dispersal, in males (1.0=litter mean).



5.5 DISCUSSION

The hypothesis that social play strengthens an individual's ties to its social group was not supported by the behaviour of young meerkats. The prediction that individuals living in large groups should play more frequently than those in small groups, because they need to reinforce ties with a greater number of partners, was not met, with no correlation between frequency of play and group size. It is possible that time or nutritional constraints (Chapter 2) prevented individuals in large groups from playing more frequently, and that such animals compensated for the presence of additional group members by distributing their quota of play across a greater number of partners. This was not the case, however, with mean number of play partners unrelated to group size. Young meerkats did not play with more than half the members of their group (for example, females devoted only 0.03% of their play interactions to the group's dominant female), and the majority of a youngster's play bouts were shared with littermates only (Fig. 4.1). Even within litters, however, individuals did not compensate for number of potential partners, with no correlation between frequency of play and litter size. Although it is not surprising that group size failed to dictate either an individual's frequency of social play or patterns of partner choice (e.g. Thompson 1998), this finding would not be anticipated if the primary function of social play in meerkats was the strengthening of group-wide social ties.

If social play enhanced affiliative ties between group members (presumably by providing strong, positive social conditioning; Baldwin 1982), social play should be associated with both an increase in affiliative interactions, and a reduction in aggressive interactions, among playmates. This, however, was not the case. A prior study (Chapter 3) found that frequency of play was unrelated to frequency of aggression in meerkat pups, and that favoured play partners were just as likely to fight one another over food as pups that played together infrequently. Similarly, pairs of pups that had just shared a play bout were no less aggressive toward one another, during the next 10 minutes, than pairs that had not played. In the current study, the prediction that frequency of social play should be positively related to the frequency of other affiliative interactions was assessed using data on allogrooming interactions. Although the affiliative role of allogrooming (Seyfarth & Cheney 1984; Dunbar 1991; Harris & White 1992; Schino 2001) has yet to be established quantitatively in meerkats, its existence is supported by the observation that subordinate meerkats incorporate allogrooming in their displays of submission (Chapter 8), and the group's dominant animals actively interrupt the allogrooming bouts of potential rivals (pers. obs.). However, this study found no correlation between rate of play and allogrooming; in fact, meerkats that played together most frequently (i.e. littermates) were less likely to share allogrooming interactions than animals that played together rarely (i.e. older group members; Chapter 4). This finding is similar to those obtained in other studies that have compared partner preferences during play and other affilitative social behaviours (Lee 1983; Watson 1993), suggesting that social play is not used as an affiliative mechanism.

Contrary to the hypothesis's third prediction, social play did not have a positive effect on an individual's contribution to group activities, either concurrently (in subadults), or as a delayed effect (Martin & Caro 1985) in adults. While a noncausal positive relationship might have been anticipated, because nutritional status is positively related to both helping behaviour (Clutton-Brock et al. 2002) and rate of play (Chapter 3) in meerkats, differences in body weight were minimal between littermates, and weight was not correlated with intralitter variation in either play or most measures of helping. Although it is possible that helping behaviour in a cooperative species is not a reliable measure of an individual's level of 'bonding' to its group, because hormonal mechanisms (Asa 1997; Ziegler 2000; Nunes et al. 2001; A.A. Carlson unpublished data), or even social factors (Zahavi & Zahavi 1997) may override individual variation in 'bonding', male meekats do reduce their contribution to pup-rearing and burrow maintenance prior to dispersal (Clutton-Brock et al. 2002), presumably reflecting their weakening ties to the group.

The final prediction generated by the social cohesion hypothesis - that an individual's frequency of play should be positively correlated with age at dispersal - was also not met. While studies of gorillas, *Gorilla gorilla* (Harcourt & Stewart 1981), and red foxes, *Vulpes vulpes* (Harris & White 1992), suggest that involvement in nonagonistic social interactions may influence an individual's decision to disperse, there has been no quantitative assessment of play's role, apart from the unsuccessful attempt to find a consistent relationship between sex differences in play and philopatry or dispersal (Smith 1982; Waterman 1986, 1988; Jamieson & Armitage 1987). Although an individual's decision to disperse is likely to be affected by many external parameters (such as the availability of co-dispersers, potential breeding partners, territorial vacancies or food), the impact of these confounding variables can be minimized by evaluating intralitter differences in behaviour, because littermates are normally exposed to a similar set of parameters. Another potential confounding variable is body condition, because it is known to influence both dispersal (Holecamp 1986) and play (Nunes et al. 1999; Chapter 2) in a number of species. However, in meerkats, body condition does not influence female dispersal (neither the likelihood of eviction or dispersal; Young 2003), and although its role in male dispersal has yet to be assessed, this study found no relationship between relative weight (prior to adulthood) and relative age at dispersal, for either sex.

In meerkats, the proximate cause of dispersal differs with sex, enabling us to assess the effect of play on both an individual's fidelity to its group, and other group members' allegiance to an individual. Since female meerkats are forcibly evicted from their natal group by the dominant female (usually with assistance from the whole group), it might be anticipated that young females that spent more time playing with their dominant female, or with a broad spectrum of group members (rather than just littermates), would be less prone to aggression from these animals, and more able to delay eviction. However, this was not the case, and relative age at first eviction, or ultimate dispersal, was unrelated to play. This result is consistent with the finding of Chapter 3: i.e. that play did not reduce aggression between meerkat pups competing for food. Unlike females, male meerkats normally disperse from their natal group without coercion, with some remaining for up to 4 years. In littermates, there was a positive correlation between age at first prospecting foray and age at dispersal (Fig. 5.2), suggesting that some individuals may be pre-disposed to an early departure from their natal group (since all littermates are exposed to similar opportunities for prospecting or dispersal). However, these early dispersers played no less frequently as youngster than their later-dispersing brothers. The tendency for male meerkats to leave their natal group to go on prospecting forays (whether measured as frequency of forays or age at first foray) was also not related to how much they had played as youngsters.

Before accepting the negative findings of this study, we need to consider whether sample sizes were large enough to allow the null hypothesis to be rejected if a biologically meaningful relationship between play and social cohesion had occurred. A power analysis of the study's main findings revealed that the tests that used individual data (deviations from same-sex mean) generally had sufficient power to confidently reject the null hypothesis, 80% of the time, if frequency of play had accounted for 20% of the variability seen in social cohesion measures. However, the validity of such post-hoc power analyses is questionable (Hoenig & Heisey 2001), and it may be more appropriate to simply note that the data did not show any positive trends; in fact, of all tests that resulted in a positive correlation coefficient (positive correlations having been predicted by the hypothesis), only one had a P value of less than 0.4.

In conclusion, there is no evidence to suggest that social play strengthens a young meerkat's ties to its group, thus enhancing social cohesion. This result corroborates the findings of interspecific comparisons (Biben 1983; Pellis & Iwaniuk 1999) in which play and degree of sociality were found to be unrelated. Although a study such as this - which examines a single species - cannot hope to identify the function of mammalian play, because play may be multi-functional (Suomi 1982; Coppinger & Smith 1989), the *negative* findings of this study are of considerable significance. As members of the mongoose family, meerkats do not enjoy a phylogenetic history of sociality (Veron et al. 2003), yet they are entirely dependent on social cohesion and cooperation for their survival. Under such circumstances, one would expect the species to strongly favour any behaviour pattern that increased an individual's commitment to its group; and the finding that meerkats do *not* use social play in this way provides compelling evidence that play behaviour is not capable of generating the physiological responses needed to increase social cohesion.

CHAPTER SIX

PLAY FIGHTING DOES NOT AFFECT SUBSEQUENT FIGHTING SUCCESS IN WILD MEERKATS

(*Animal Behaviour*, in press)

6.1 ABSTRACT

Despite more than three decades of research, the adaptive significance of play behaviour remains unknown. The practice hypothesis asserts that the primary function of play is to provide animals with the opportunity to practice and refine motor skills needed in adulthood. The apparent similarity between play fighting and serious fighting has led to the assertion that play is 'optimally designed' for the enhancement of combat skills. However, the practice hypothesis of play fighting has never been tested. This study used data from a wild population of meerkats, *Suricata suricatta* (a cooperatively breeding mongoose that shows marked reproductive skew), to examine whether play experience improved an individual's subsequent fighting ability. Firstly, I established that meerkats showed no sex difference in frequency of play fighting (consistent with the optimal design argument, since both males and females fight to obtain the dominant breeding position in a group). Secondly, I established that frequency of play fighting was not positively correlated with the subsequent likelihood of winning play fights, or the degree of improvement in play fighting success, as would be expected if play improved fighting manoeuvres (and such manoeuvres must be the same both in play fighting and serious fighting if motor skills are to be effectively practiced). Finally, I established that individuals that ultimately won fights for a vacant dominancy did not play fight any more frequently as youngsters, or show any greater success in winning play fights, than matched same-sexed littermates that they defeated in combat.

6.2 INTRODUCTION

Despite more than three decades of research, the adaptive significance of play behaviour remains one of the greatest enigmas in ethology (Barber 1991; Spinka et al. 2001). Of the 30 or more hypotheses postulated to explain play's function (Baldwin & Baldwin 1977), the practice hypothesis (Groos 1898) is the most enduringly popular (Fagen 1981; Smith 1982; Caro 1988). This hypothesis asserts that play gives young animals the opportunity to practice and refine motor skills that they will need in adulthood. Play fighting, prominent in the play of numerous taxa (Fagen 1981; Smith 1982), is believed to enhance an animal's combat skills (e.g. Symons 1978; Byers 1980; Pellis 1981; Jamieson & Armitage 1987; Rothstein & Griswold 1991; Watson & Croft 1993; Miller & Byers 1998), and the apparent similarity between play fighting and real fighting (Fagen 1981), has led to the assertion that play is 'optimally designed' (Martin & Caro 1985) for the practice of fighting skills (Smith 1982). Consistent with this argument is the finding that males in sexually dimorphic, polygynous species generally engage in more serious fighting, and more play fighting, than females (Smith 1982). Nevertheless, no attempt has been made to assess the effects of play fighting experience on subsequent fighting ability. As noted by Smith (1982, pp. 144), 'the best direct test of the fighting skills hypothesis would be to show that high levels of play fighting in infancy are linked to better skills and success as an adult.' Bekoff (1982, pp. 156) went on to add, 'furthermore, and of critical importance, one would also have to demonstrate that better fighting skills, acquired through play, are associated with increased reproductive success – a tall order!' This study partially fulfills this order, using data obtained from a wild population of meerkats, *Suricata suricatta*.

Meerkats are diurnal, desert-adapted mongooses that live in groups of 3-40 individuals. They are obligate cooperative breeders (Clutton-Brock et al. 2001a), and a group's dominant breeding pair parent around 75% of all pups successfully reared by the group (Griffin et al. 2003). Dominance of a group is normally attained through fighting, in both sexes, and dominance battles often result in quite serious injury (personal observation). In this study, I use three approaches to assess whether play experience improves an individual's fighting ability. Firstly, I establish whether meerkats show a sex difference in play fighting, since the optimal design argument predicts equal participation in play by both sexes, because meerkats are not sexually dimorphic (Clutton-Brock et al. 2002) or polygynous, and both sexes use combat to gain dominance of a group which then provides them with the same huge fitness benefits.

My second approach recognizes that the motor patterns undertaken during play fighting and real fighting must be the same (although potentially broken up or reordered in play), if play is to provide effective practice for combat (Stamps 1995; Byers 1998). Therefore, an individual that is skilled at these motor patterns (or fighting manoeuvres) should be successful at both real fighting and play fighting (assuming individuals generally play to win; Thompson 1998). I thus examine whether the amount of time a young meerkat devotes to play (i.e. time spent practicing) is positively related to its subsequent ability to win play fights, or the degree to which its play fighting ability improves over time.

Finally, I examine whether individual differences in play experience can account for subsequent differences in success during serious fighting, by comparing the play histories of meerkats that have won dominance of a group, with the histories of littermates which they defeated in combat. I test whether winners had, as youngsters, 'practiced' (i.e. played) more often, or exhibited higher rates of success at play fighting, than their defeated siblings. I also examine whether any asymmetry in play fighting ability apparent during the matched pair's shared play interactions was predictive of the outcome of their later fight for dominance.

6.3 METHODS

6.3.1 Study population

Data were collected between April 1996 and November 2002 from a wild population of meerkats living on ranchland in the southern Kalahari Desert, 30 km west of Van Zylsrus, South Africa (26°58'S, 21°49'E). See Section 1.6 for details of the study site's topography, vegetation and rainfall. The study was carried out under licenses issued by the Northern Cape Conservation Service, South Africa. Seventy-six individual meerkats from 14 groups contributed to the data. All meerkats were habituated to close observation and handling, and were individually marked with permanent marker pen on the tail, or with a small patch of lightly trimmed fur. These marks were applied unobtrusively while the animals stood sunning in the mornings. Age classes were defined as follows: pup, less than 3 months old; juvenile, 3-6 months old; subadult, 6-12 months old; and adult, over 12 months old.

During the study, 18 pairs of same-sexed littermates were known to have fought one another for the dominance of a group. Fights were either observed directly or ascertained by the bite wounds (mainly on the face and neck) exhibited by contestants for dominance. All animals were fully mature at the time of their dominance fight (mean age 27.4 +/- 2.4 months, N=36), and winners were readily identified by their prolific scent-marking behaviour (Gsell 2002) and frequent intimidation of defeated competitors. Because documented fights between littermates were relatively uncommon, and almost invariably occurred after the animals had dispersed, the data points for this study were obtained opportunistically over a 6.5-year period, and not all 18 matched pairs of littermates were sampled for all measures used in the analysis (exact sample sizes are outlined below).

6.3.2 Frequency of play

I used two methods to quantify the frequency of play in young meerkats. To measure rate of social play in pairs of same-sexed littermates (that ultimately fought each other as adults), I used instantaneous scan sampling (Altmann 1974), recording the behaviour of both littermates at 10-minute intervals. I defined social play (also referred to as play fighting) as play involving mutual bodily contact between two or more animals. Instantaneous scan sampling was undertaken for approximately 3 hours each morning, with an average of 54 +/- 8 hours of data collected for each of 12 pairs of pups (four male and eight female), 73 +/- 9 hours for each of 12 pairs of juveniles (six male and six female), and 140 +/- 23 hours for each of 13 pairs of subadults (six male and seven female).

Due to the relative rarity of play, it was not feasible to use instantaneous scan sampling to document the detailed age/sex distribution of play, because a larger number of scans was required than I could collect on a monthly basis. I therefore used one/zero scan sampling (Martin & Bateson 1986) with a sample interval of 20 seconds (i.e. I recorded every 20 seconds whether each pup in the litter had played during the preceding 20 seconds). I documented the presence/absence of three types of play: locomotory play (solitary leaping, running or prancing), object play (play incorporating an object, such as carrying a feather or tugging at vegetation) and social play (also referred to as play fighting; as defined above). I collected *these* data once the meerkat group had emerged from its sleeping burrow around sunrise and stopped sampling when the group set off to forage, usually 15-90 minutes (mean 37 minutes) later. I targeted this period at the burrow because it is the time at which meerkats play most reliably. I collected one/zero scan data for eight litters of meerkats (37 individuals: 19 males and 18 females) from six groups. On average, I collected 4.8 +/- 0.18 mornings of data for each individual per month throughout their first year of life, beginning at 4 weeks of age. Four of the eight litters were also sampled when they were less than 1 month old, before they left their natal burrow. In the analysis of one/zero scan data, I averaged the daily rates of play for each individual each month, and then obtained mean litter rates (total, male and female) by averaging the rates of individual litter members. Although I refer to the percentage of one/zero scan intervals in which an individual played as its rate of play, one/zero scan sampling does not provide a true measure of frequency. Nevertheless, there was a significant correlation between the relative rate of play fighting obtained using one/zero sampling and that obtained using instantaneous scan sampling for the seven litters of pups that were sampled by both means (Spearman rank correlation: r_s=0.512, N=28, P=0.006).

I also used this one/zero scan sampling data when examining the effect of frequency of play on improvement, or subsequent success, in play wrestling (see definition below). For this analysis, I collected one/zero scan data for one additional litter of juveniles (comprised of two males and five females) and, in the analysis, averaged an individual's daily one/zero values for an entire age period (i.e. pup, juvenile and subadult).

6.3.3 Play fighting roles

To document the roles that individuals adopted during play fights, I recorded play bouts ad libitum (Altmann 1974) whenever social play was observed. Individual play bouts tended to be very short, and I considered a bout concluded if a pair ceased playing for more than 5 seconds. For each social play bout I recorded the identity of the play partners as a dyad, and although additional meerkats took part in approximately one-fifth of bouts, the two protagonists were clearly identifiable due to the one-on-one nature of the play. A detailed description of the behavioural components of meerkat social play can be found in Wemmer & Flemming (1974). In this study, I recorded all observed instances of wrestling (one animal lies on its back while the other stands on or over it, pinning it to the ground; Fig. 4.1a), as well as chasing and fleeing. I refer to the dominant 'on-top' wrestling position as the winning position and the submissive 'on-the-bottom' position as losing (Thompson 1998). Role reversals did sometimes occur within a single play bout, in which case both players were credited with both winning and losing the wrestling bout, and hence percentages do not necessarily add to 100.

I recorded play fighting roles for the eight main study litters plus one additional litter (one male and four females) throughout their first year of life, beginning at 1 month of age (totalling 42 meerkats: 20 male and 22 female). Four females, however, did not survive to their first birthday, with two excluded from the analyses of juveniles and four from the analysis of subadults. I also documented the play fighting roles of one additional litter of pups (two males and one female), one additional litter of subadults (two males and two females) and one additional litter (two males and five females) as both juveniles and subadults. In all, I recorded 27,100 play bouts, with an average of 377 +/- 19 bouts collected for each individual pup (*N*=45), 246 +/- 15 bouts per juvenile (*N*=47) and 208 +/- 14 bouts per subadult (*N*=49).

Play role data was available for seven matched pairs of same-sexed littermates that later fought for dominance of a group (three male dyads and four female dyads, from six litters). When assessing these individuals' overall degree of play fighting success, I included in the analysis all play bouts undertaken by the individual regardless of the identity of its play partner (mean 733 +/- 90 bouts per individual), but when examining asymmetry in the play fighting ability of a matched pair of littermates, I restricted the analysis to bouts that the two individuals had shared together (mean 154 +/- 30 bouts per dyad).

6.3.4 Weight

Weight measurements were taken for 13 matched pairs of littermates during the 3 weeks prior to their fight for dominance. Animals were weighed in the mornings before they began foraging, by enticing them on to an electronic balance with a crumb (<0.5g) of hard-boiled egg. On average, 6.2 +/- 0.5 measurements were taken per individual, and these were averaged to obtain an individual's weight at fighting.

6.3.5 Analysis

To assess the relationship between frequency of play and improvement, or subsequent success, in play wrestling, I pooled data for individuals from different litters, and used 'deviation from same-sex litter mean' to standardize for litter. This measure was obtained by dividing the value recorded for an individual by the mean value for all same-sexed animals in its litter (hence a value of one equals the mean). I chose this method of standardization because it corrects for interlitter differences caused by such factors as litter size, group size and composition, habitat type, prey abundance, etc., but maintains interlitter differences in variance (caused primarily by individual differences between littermates). All references to 'relative' values refer to deviations from same-sex litter mean. Individuals that had no same-sexed littermates were excluded from such analyses (reducing female sample sizes by three).

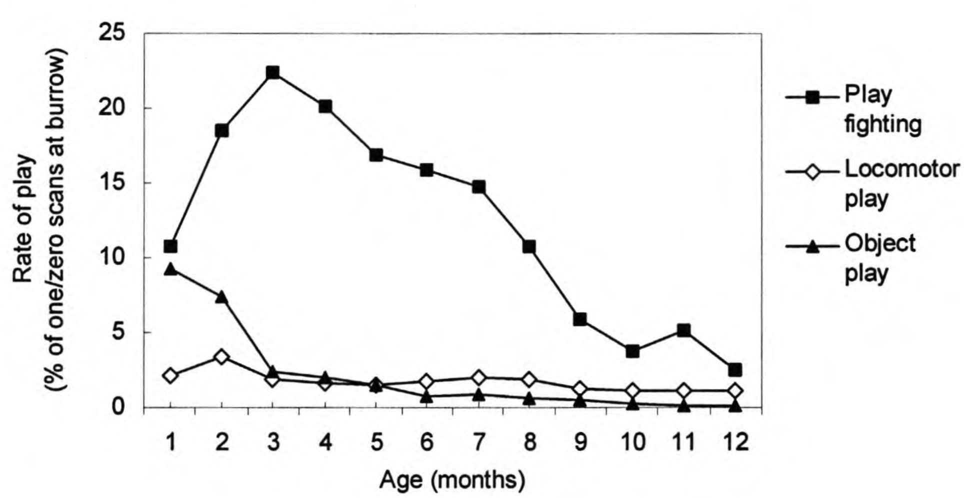
I used parametric statistical tests throughout the analysis except where the data differed significantly from a normal distribution (based on the Kolmogorov-Smirnov test for normality). In these cases, I used equivalent nonparametric tests. All statistical tests were two-tailed, with a significance threshold of 0.05. Means are given +/- SE.

6.4 RESULTS

6.4.1 Sex differences in play

Meerkats undertook play fighting more frequently than other types of play, with levels peaking at around 3 months of age (Fig. 6.1). In contrast, frequency of locomotory play remained fairly constant throughout the first year of life, and rates of object play fell to low levels after 2 months of age (Fig. 6.1). The sexes did not differ in their rate of total play, locomotor play, object play or social play (Fig. 6.2), at any age.

Figure 6.1. Mean frequency of different types of play in meerkats, by age. (N = 8 litters; except for month one: N=4).



Young meerkats undertook play wrestling during 39 +/- 2% of their play fighting bouts. In pups and subadults, there was no difference between the sexes in the likelihood of wrestling during play, but in juveniles, males were 8% more likely than their sisters to undertake wrestling (paired t test: pups: t_9= -0.303, P=0.769; juveniles: t_9= -3.12, P=0.001;

subadults: t_{10}= -0.514, P=0.619). However, despite the males' additional wrestling experience, they became increasingly more likely to lose play wrestling bouts as they aged (Fig. 6.3).

Figure 6.2. Mean frequency of play fighting in meerkats, by age and sex (N= 8 litters; except for month one: N=4). No significant difference between the sexes at any age.

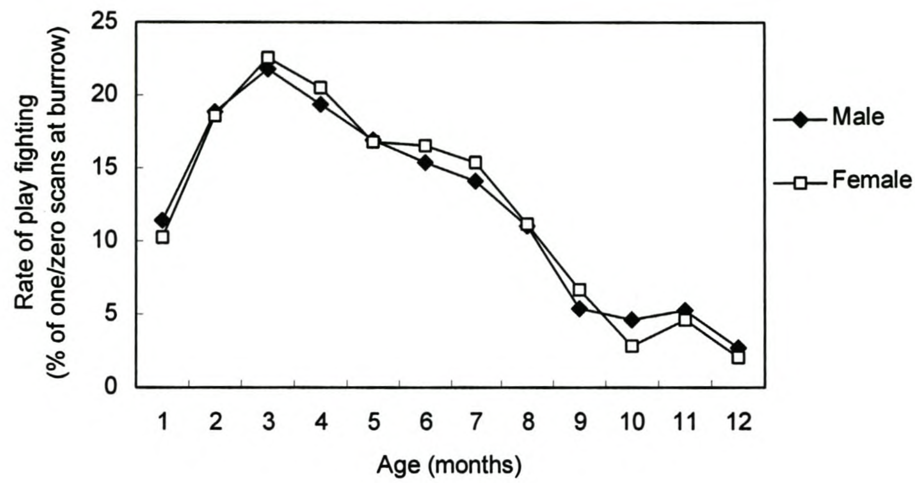
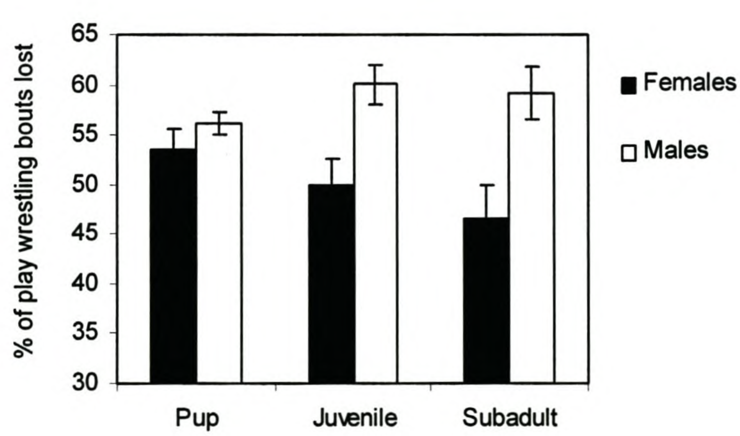


Figure 6.3. Mean percentage of total play wrestling bouts in which the losing 'on-bottom' position was adopted, by sex (paired t test: pups: t_9= -0.976, P=0.355; juveniles: t_9= -2.727, P=0.023; subadults: t_9= -2.715, P=0.022). Vertical lines indicate SE.



6.4.2 Does practice make perfect?

Young meerkats that played more frequently than their same-sexed littermates were no better at attaining the dominant wrestling position during play, later in life, than those that played infrequently. Relative frequency of play fighting in pups, of either sex, was unrelated to the relative likelihood of attaining the winning position when play wrestling as a juvenile (males: Spearman correlation: r_s= -0.202, N=19, P=0.401; females: Pearson correlation: r_{11}= -0.173, P=0.572), and the same was true of frequency of play as a juvenile and subsequent success as a subadult (Pearson correlation: males: r_{19}=0.297, P=0.191; females: r_{16}=0.257, P=0.303).

Young meerkats that played more frequently than their same-sexed peers also failed to show any greater improvement in their ability to win play wrestling bouts. Relative frequency of play fighting in juvenile meerkats, of either sex, was not correlated with percentage change in the proportion of play wrestles won, from the juvenile period to the subadult period (males: Spearman correlation: r_s=0.117, N=21, P=0.633; females: Pearson correlation: r_{16}=0.266, P=0.285). Relative frequency of play in pups was also unrelated to improvement in winning of play wrestles, from pup to subadult, in females (Pearson correlation: r_{11}=0.404, P=0.171) and was actually negatively correlated in males (Spearman correlation: r_s= -0.534, N=19, P=0.019).

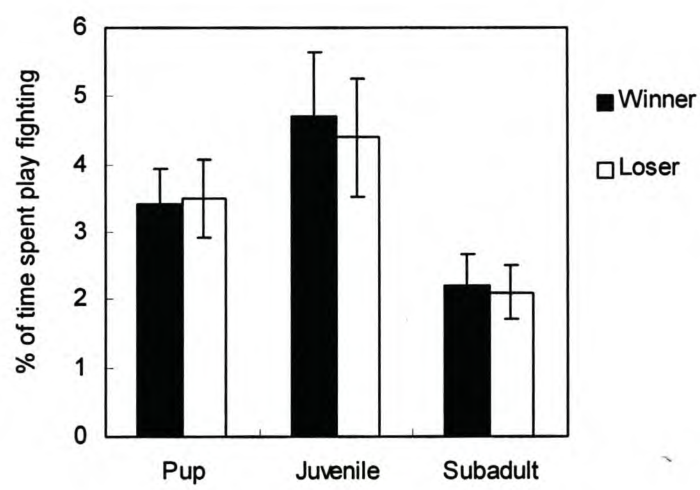
The amount of time a young meerkat devoted to play fighting also appeared to have no effect on its subsequent likelihood of winning a serious fight. There was no significant difference in the frequency of play fighting shown by individuals that proved successful fighters as adults and those that did not (Fig. 6.4). Winners of dominance battles spent 3.4 +/- 0.5% of their time play fighting as pups compared with 3.5 +/- 0.6% for losers, 4.7 +/- 0.9% compared with 4.4 +/- 0.9% as juveniles and 2.2 +/- 0.5% compared with 2.1 +/- 0.4% as subadults (Fig. 6.4). Small sample sizes were unlikely to have been responsible for this negative result, because increasing the sample size by 40% (through the incorporation of win/lose pairs whose rate of play was measured using one/zero scan sampling, and then testing the data nonparametrically) actually increased the P values for this analysis.

6.4.3 Success in play fights versus real fights

An individual's likelihood of winning play fights during its first year of life (and thus, hypothetically, its skill in fighting manoeuvres) appeared to be unrelated to its likelihood of winning a real fight for dominance later in life. Winners of serious fights had attained the dominant, on-top wrestling position during 56.8 +/- 2.8% of their play wrestling bouts compared with 53.7 +/- 2.3% for the losers of serious fights (paired t test: t_6=0.971, P=0.369). Similarly, winners and losers of real fights were equally likely to have adopted the chasing role during play interactions that included chase/flee behaviour (paired t test: t_6=0.948, P=0.380).

A dyad's play relationship also did not reflect the pair's subsequent dominance relationship. Individuals that defeated a littermate in a dominance fight were no more likely than their defeated sibling to have won the play fights that the two had shared prior to adulthood. Winners of serious fights attained the dominant position during 57.7% of the two's shared play wrestling bouts, compared with 52.8% for losers (paired t test: t_6=0.651, P=0.539). Winners and losers were also equally likely to have adopted the chasing role during their chase/flee play interactions (paired t test: t_6=1.023, P=0.346).

Figure 6.4. Frequency of play fighting (prior to adulthood) in meerkats that ultimately won a fight for the dominant position within a group, and in same-sexed littermates that they defeated (pups: paired t test: t_{11}= -0.137, P=0.894; juveniles: Wilcoxon signed-rank test: W= -17.00, N=12, P=0.432; subadults: paired t test: t_{12}=0.412, P=0.687).



It is conceivable that these negative findings were the result of an erroneous acceptance of the null hypothesis due to small sample sizes. However, a post-hoc power analysis (Thomas & Juanes 1996) of the statistical tests used to compare success in play fights with success in serious fights found they had sufficient power to confidently reject the null hypothesis (80% of the time) if winners and losers of serious fights had differed in their level of play success by 10-20%. Nevertheless, because the validity of post-hoc testing is questionable (Hoenig & Heisey 2001), it may be more useful to note that the data showed no visible trend, and in at least three of the seven matched pairs, winners of serious fights were less successful during play than their defeated siblings.

An individual's size, relative to its partner, did not affect the outcome of fights for a vacant dominant position. Weight differences between littermates at the time of combat were small (mean 6.1 +/- 1.14%; range=0.6–12.0%; N=13) and individuals that won dominance battles were neither significantly heavier nor lighter than their defeated siblings (paired t test: t_{12}=1.143, P=0.275).

6.5 DISCUSSION

Meerkats are obligate cooperative breeders that show marked reproductive skew (Clutton-Brock et al. 2001a) so winning the dominant breeding position within a group provides high fitness benefits, for both sexes. Once established, a dominant can expect to hold its position for life (although challenges and reversals do occasionally occur among males) and to monopolize three-quarters of the reproductive effort generated by the whole group (Griffin et al. 2003). Clearly, there is a strong adaptive advantage in maximizing fighting ability in this species, and if play is capable of enhancing combat skills, meerkats should be capitalizing on this trait. Nevertheless, this study found no evidence that play fighting improved subsequent combat skills. Meerkats that devoted more time to play fighting than their littermates were no more successful at winning subsequent fights (either in a serious context or in play) than those that played infrequently. This was not the result of poor fighters playing more often (to accrue the skills they lacked) because frequency of play was not negatively correlated with concurrent play fighting success, in meerkats of any age (L. L. Sharpe unpublished data), and nor was it positively correlated with improvement in play fighting success as would be expected if individuals were using play in this way.

It is possible that an individual's level of fighting skill was masked during play by self-handicapping (i.e. allowing the weaker player to win; Aldis 1975). However, there is strong evidence to suggest that animals 'play to win' or, at least, strive to avoid losing. In many species (e.g. Owens 1975; Symons 1978; Byers 1980; Hole 1988; Boulton 1991; Biben 1998) individuals are more likely to initiate play with partners that they can defeat, and avoid playing with those that are likely to beat them. Similarly, in both meerkats (Chapter 3) and squirrel monkeys, *Saimiri sciureus* (Biben 1989), individuals that are unlikely to win a play fight avoid taking part in 'directional' play wrestling (where one partner wins by pinning the other down), and instead favour 'nondirectional' forms of play fighting. Many taxa also show a strong preference for play partners that are closely matched in size (e.g. Brueggeman 1978; Berger 1980; Byers 1980; Stevenson & Poole 1982; Boulton 1991; Watson 1993; Thompson 1996; Chapter 7) consistent with the argument that individuals are attempting to maximize their likelihood of winning. In meerkats, play fighting success appears to genuinely reflect competitive ability, because the win-lose asymmetries seen in the play of pups are positively related to asymmetries observed during squabbles over food (Fig. 7.1), and, in older animals, play fighting success appears to reflect an animal's status within the group (Chapter 9), explaining why females (which are socially dominant to males; Chapter 8), win a higher proportion of play fights (Fig. 6.3). If self-handicapping is not a prominent feature of meerkat play, the finding that a dyad's win-lose asymmetries during play did not predict the outcome of the pair's subsequent fight for dominance, suggests that the skills required to win serious fights are different from those employed during play.

Obviously, many factors other than play experience are likely to affect the outcome of a critical fight for dominance. We know that play fighting is not requisite for the development of serious aggressive behaviour (e.g. in a number of species, siblings fight for dominance prior to the ontological appearance of play fighting; McBride 1963; Bekoff 1974; Byers 1984; Drea et al. 1996), and the relatively subtle benefits produced by 'practice' may be obscured by other factors, such as disparity in size, age, social experience, health or nutritional status. However, by limiting comparisons to littermates (same-aged individuals that have been subjected to similar nutritional, social and physical parameters throughout their lives), this study minimized such confounding variables, and yet still found no evidence that play experience increased an individual's likelihood of winning.

Although numerous detailed studies of play have concluded that the most likely function of play fighting is the practice of combat skills (e.g. Symons 1978; Byers 1980; Pellis 1981; Jamieson & Armitage 1987; Rothstein & Griswold 1991; Watson & Croft 1993; Miller & Byers 1998), none of these studies have attempted to test the hypothesis, and their conclusions spring from arguments of design and/or a paucity of evidence to support alternative hypotheses. Although the results of this study also fulfilled the prediction generated by the design argument (i.e. meerkats showed no sex difference in frequency of play), to quote Ghiselin (1982, pp 165), 'a mere correlation between what an animal does in play and in other activities constitutes most dubious grounds for invoking practice as a cause.' The design argument for practice has further been weakened by the finding that, in several species of rodent, the targets of attack and defense used in play differ from those adopted in serious fighting (Pellis 1988; 1993). Since the effective practice of a motor skill requires the repetition of the *exact* same motor pattern (Stamps 1995), play fighting cannot assist in the refinement of fighting skills in these species. It has also been noted that the most difficult manoeuvres undertaken during real fighting (e.g. blocking an attack) are usually absent from play fighting (Biben 1998; Pellis & Pellis 1998), thus making play a poor candidate for the practice of combat skills.

While a study such as this cannot entirely rule out the possibility that meerkats gained some benefit from 'practicing' fighting manoeuvres in play, any such gain was, at best, too small to detect. However, play in young meerkats is known to carry an energetic cost, with energy invested in play almost certainly diverted from growth (Sharpe et al. 2002). Since juvenile meerkats that are heavier than their peers enjoy many downstream advantages (being more likely to breed in their natal group and more likely to gain dominance of a group; Clutton-Brock et al. 2001b), it seems unlikely that a young meerkat would sacrifice these clear fitness benefits (by 'playing away' energy that it could invest in growth) for nothing more than a negligible enhancement of fighting ability.

Although this study was restricted to a single species (albeit one in which fighting ability is closely allied with reproductive fitness), its findings must cast considerable doubt upon the hypothesis that play fighting functions to practice adult combat skills, and should sound a warning against the general acceptance of a hypothesis, however intuitively appealing, that has not been quantitatively tested. The study's negative findings are also consistent with those obtained by researchers examining the downstream effect of variation in play experience on prey-catching ability in predatory species (Thomas & Schaller 1954; Vincent & Bekoff 1978; Caro 1980; Davies & Kemble 1983), or on skill at sensorimotor and social tasks in captive common marmosets, *Callithrix jacchus jacchus* (Chalmers & Locke-Haydon 1984). All in all, it seems most unlikely that the primary function of play in young mammals is the practice and refinement of adult motor skills.

CHAPTER SEVEN

DO MEERKATS USE PLAY FOR SELF-ASSESSMENT?

7.1 ABSTRACT

The self-assessment hypothesis of play postulates that play provides animals with immediate feedback about their own physical capabilities, thus allowing them to modify their development appropriately, and assisting them in the assessment of risk. This study examined whether the predictions about play partner preferences generated by the self-assessment hypothesis were fulfilled by the behaviour of young meerkats, *Suricata suricatta*, in a wild population. The study found that meerkats strongly favoured same-aged play partners but, although partner preferences were generally maintained across development, fidelity to a favourite individual did not occur. During the peak period of social play (prior to 6 months of age), disparity in both size and play fighting ability were negatively correlated with degree of preference in dyads of same-aged animals, and change in level of disparity in ability was negatively correlated with change in degree of preference. In mismatched littermate dyads, play was just as likely to have been initiated by either partner, suggesting that rivalry for dominance was not motivating partner choice in this age group. In older meerkats (6-12 months), the predictions of the self-assessment hypothesis were not met and other factors (e.g. a growing awareness of social status) were governing partner choice. The study concluded that although young meerkats preferred well matched play partners, individuals did not appear to use information gained in play to modify either their own play behaviour or their dealings with playmates, and because play appears not to be the most appropriate behaviour for use in self-assessment, this is unlikely to be its primary function in this species.

7.2 INTRODUCTION

Despite more than three decades of research and the postulation of numerous hypotheses, the adaptive function of play behaviour remains obscure (Spinka et al. 2001). The self-assessment hypothesis (Thompson 1996, 1998) suggests that play provides animals with immediate feedback about their own physical capabilities, with young animals testing their abilities by repeatedly performing increasingly challenging locomotor or social actions in play. The feedback they obtain about their performance allows them to modify their own development appropriately, and assists in their assessment of risk (Thompson 1998). Although the ultimate benefits of self-assessment remain ill defined and are most likely to be cognitive (Spinka et al. 2001), making the testing of outcomes difficult, the hypothesis makes a number of falsifiable predictions about the structure of play behaviour, particularly the choice of partners during social play (Thompson 1998).

According to the self-assessment hypothesis, social play (especially play fighting) is inherently competitive (Biben 1998, Thompson 1998) and thus provides an unprecedented opportunity for social comparison. Because competitive play between same-aged youngsters (i.e. those at the same stage of development) allows an animal to readily detect any shortcomings in its own development, individuals should favour play with peers, and should maintain their preference for particular partners consistently over the course of development (Thompson 1996, 1998). Animals will also obtain the most sensitive feedback (about nuances in their ability) from play partners that are well matched for size (strength) and skill, and play between mismatched animals (in which one individual always wins) will provide neither individual with much information about small changes in its own ability. Therefore, any change in level of matching between two individuals should be reflected in a change in degree of preference and, in mismatched pairs, both the winner and the loser should be equally disinterested in playing together. The self-assessment hypothesis also suggests that the testing provided by play is progressive (Thompson 1998) – i.e. when an individual successfully masters one play 'task' (or, in the case of competitive social play, one partner), it progresses to a more difficult challenge. Conversely, if an individual is unable to succeed at a given task (or with a particular play partner), it will shift to a less demanding challenge.

This study examines whether the patterns of social play observed in a wild population of meerkats, *Suricata suricatta,* meet the predictions generated by the self-assessment hypothesis. If self-assessment is an important factor in determining play partner choice in young meerkats, one would expect the following: (1) individuals will prefer to play with partners that are closely matched for age, size and ability; (2) well-matched, same-aged play partners will maintain a stable preference consistently over the course of development; (3) when a pair of individuals are unevenly matched, both animals will be equally disinterested in playing together; (4) if the level of disparity between play partners changes, preference for that partnership will alter accordingly; (5) individuals that are highly successful during play with peers will seek more challenging play partners, and those that repeatedly lose will favour easier partners.

7.3 METHODS

7.3.1 Study population

I collected data between August 1999 and September 2001, from a wild population of meerkats living on ranchland in the southern Kalahari Desert, 30 km west of Van Zylsrus, South Africa (26°58'S, 21°49'E). See Section 1.6 for details of the study site's topography, vegetation and rainfall. The study was carried out under licenses issued by the Northern Cape Conservation Service, South Africa.

Meerkats are diurnal, desert-adapted, social mongooses that live in close-knit groups of 3-40 individuals. Groups are normally comprised of a dominant breeding pair, the pair's offspring (which delay dispersal until around 2 years of age; Chapter 5) and several immigrant males (Clutton-Brock et al. 2001b). During periods of non-drought, meerkat groups raise up to 4 litters of pups annually (mean litter size 4.1), with an interbirth interval of 73-143 days (Russell et al. 2003a). All meerkats included in the study were habituated to close observation and handling, and were individually marked with permanent marker pen on the tail, or with a small patch of lightly trimmed fur. These marks were applied unobtrusively while the animals stood sunning in the mornings. Data were collected for 52 study individuals (from ten litters) in seven groups. Three of the study litters were comprised of pups borne by more than one female, but the youngsters were raised together as a single litter, and were treated as such in this study. Age classes were defined as: pup, less than 3 months old; juvenile, 3-6 months old; subadult, 6-12 months old (when sufficient data were available, this class was subdivided into subadult 1, 6-9 months old, and subadult 2, 9-12 months old); and adult, over 12 months old.

7.3.2 Body weight

All meerkats included in the study were weighed approximately three times each week, before they began to forage in the mornings, by enticing them on to an electronic balance with a crumb (<0.5g) of hard-boiled egg. To calculate weight differences between individuals within a litter, I divided each age period (pup, juvenile, subadult) into 2-week blocks, averaged an individual's weight measurements for each 2-week period, and then expressed the difference between its mean weight and that of each of its littermates as a percentage of the pair's mean weight. These bi-weekly percentage differences were then averaged to obtain a value for each dyad for the entire age period. To assess mean weight differences between a study litter and the litters closest to it in age (the cohort immediately older than the study litter was, on average, 108.4 +/- 14.9 days older, while the cohort immediately younger was 79.7 +/- 0.4 days younger), I calculated the mean weight of each cohort on a bi-weekly basis, and then expressed the difference between a cohort and the study litter as a percentage of the study litter's weight. These bi-weekly values were then averaged to obtain a percentage difference for the entire age period. Two of the study litters did not possess younger siblings and were thus excluded from the analysis.

7.3.3 Play behaviour

Although meerkats of all ages indulge in play, animals under 6 months of age show the highest frequencies (Fig. 6.1), playing, on average, for 4 % of their day. Play is primarily social, taking the form of play fighting (see Wemmer & Flemming 1974 for a detailed ethogram of meerkat play, and Section 1.5.4 for a summary) and I defined play fighting (which I also refer to as social play) as play involving mutual bodily contact between two or more meerkats. Young meerkats show a strong preference for playing with littermates throughout their development, but do not favour individuals of a particular sex (Chapter 4). In this study, I documented play bouts ad libitum (Altmann 1974) whenever a study individual was observed to play with another group member. Individual bouts of play fighting were generally very short and I considered a bout finished if the pair stopped playing for more than 5 seconds. Although meerkat play was not strictly dyadic (approximately one-quarter of all play bouts involved more than two animals), it consisted of sequential interactions between pairs of animals (Thompson 1998), and I recorded the identity of play partners as a dyad, because the two main protagonists were always clearly identifiable. Whenever possible, I recorded which individual initiated the play bout, but initiations were subtle, and the initiator was discernible in less than one-third of interactions. To measure disparity in play fighting ability, I documented all observed occurrences of wrestling (in which one animal lay on its back while the other stood on or over it, pinning it to the ground) and chase/flee behaviour during play bouts, recording which partner attained the dominant, winning position (i.e. chasing, or 'on top' during wrestling). If one or more role reversals occurred during the play bout, both individuals were considered to have 'won' the bout.

I collected play data for eight of the study litters (42 individuals) regularly throughout their first 12 months of life (beginning at 1 month of age). For one litter (three individuals) I collected data during the pup period only, and for one litter (seven individuals) I collected data during the juvenile and subadult periods only. In total, I documented 28,634 play fights.

7.3.4 Analysis

I used parametric statistical tests throughout the analysis except where the data differed significantly from a normal distribution (based on the Kolmogorov-Smirnov test for normality). In these cases, I used equivalent nonparametric tests. All statistical tests were two-tailed, with a significance threshold of 0.05. Means are given +/- SE.

In the majority of analyses of play, I limited the analysis to play bouts undertaken between littermates and have used dyads of littermates as the sampling points (see Table 7.1 for sample sizes). While it could be argued that this involved psuedoreplication (because each individual was represented in more than one dyad), it was the *relationship* between the two individuals (each of which was unique) that was sampled, not the individuals per se.

Table 7.1. Number of littermate dyads sampled per age class, and number of dyads excluded from the analysis because they were not observed to undertake the behaviour in question.
* Three study animals, which died prior to adulthood, were excluded from the subadult age class.

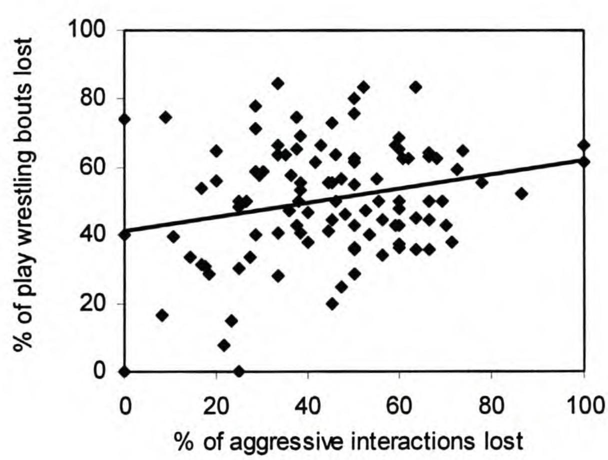
Age class	No. of dyads sampled	No. of dyads excluded:		
		wrestling	chase/flee	initiations
pups	104	0	1	0
juveniles	120	1	2	12
subadults*	115	3	6	4

To calculate disparity in play fighting ability among littermate dyads, I used the following formula:

$$\frac{Wx - Wy}{Bxy}$$

where Wx is the number of times individual x won the dyad's shared wrestling bouts, Wy is the number of times individual y won, and Bxy is the number of wrestling bouts shared by the pair (dyad xy). Hence the disparity exhibited by a dyad could range between -1.0 (all bouts won by animal y) and 1.0 (all bouts won by animal x), and a value of 0.0 indicated that the individuals were evenly matched. I also used this formula to calculate disparity in chase/flee behaviour, and play initiations for littermate dyads. For the majority of the analyses, I converted all negative disparity values to positive integers to create a nondirectional measure (degree of disparity), however, for analyses that examined the effects of winning (or of a size advantage), I maintained the negative disparity values (for both variables), and refer to this measure as 'directional' disparity. Littermate dyads that were not observed to indulge in a particular component of play were excluded from the analyses of that component, resulting in some variations in sample size (Table 7.1). Throughout the analysis I have chosen to use disparity in play wrestling success as a measure of disparity in ability, because the ability to win play wrestling bouts does appear to be related to actual competitive ability in young meerkats (Fig. 7.1), and directional disparity in both wrestling and in chase/flee behaviour were positively correlated for all age classes (Pearson correlation: pup: r_{101}=0.354, P<0.001; juveniles: r_{118}=0.232, P=0.011; subadults: Spearman rank correlation: r_s=0.306, of play shown by members of a dyad, index values can become distorted if the variation between littermates is extreme (which was not the case in this study). For example, if a litter contained an individual that rarely played with its littermates, all dyads that included that individual would show preference index values of less than one (i.e. the dyads would be considered to have played less frequently than was expected by chance). While this is not necessarily an inaccurate result with regards to the level of preference exhibited by the dyad (since choosing not to play with littermates is, in itself, an expression of preference), such index values cannot be used to assess the preferences of an individual, and I used alternative measures when identifying the most favoured play partners of individuals.

Figure 7.1. Percentage of play wrestling bouts with partner that were lost, as a function of the percentage of aggressive interactions (during social foraging) with that partner that were lost, in littermate dyads 4-10 weeks old (Pearson correlation: r_{102}=0.242, P=0.013). Refer to Section 3.3 for details of methods.



7.4 RESULTS

7.4.1 Are play partners matched for size?

The size of potential partners did appear to affect play partner choice in young meerkats. Meerkats not only strongly preferred to play with littermates (Fig. 4.1) - i.e. the group members that matched them most closely for size - but, among dyads of littermates, percentage difference in body weight was negatively correlated with play partner preference in pups and juveniles, although not in subadults (Fig. 7.2). Within littermate dyads, a size advantage was associated with success during play wrestling bouts for pups and for juveniles, but was unrelated to winning for subadults (Spearman correlation: pups: r_s=0.344, N=104, P<0.001; juveniles: r_s=0.218, N=121, P=0.016; subadult: r_s=0.123, N=112, P=0.196).

Young meerkats also played with nonlittermates, but the only group members that they favoured (i.e. played with more frequently than expected by chance) were members of the two cohorts nearest to themselves in age (Table 4.2) and hence also nearest in size. In a comparison of study litters, however, I found no relationship between the mean number of play bouts a study animal shared with a member of an adjacent cohort (relative to the mean number shared with a littermate) and the mean percentage size difference between the cohort and the study litter, at any age (Pearson correlation: pups/older cohort: r_6= -0.403, P=0.322; juveniles/older cohort: r_7=0.277, P=0.471. Spearman rank correlation: subadults/older cohort: r_s=0.008, N=9, P=0.948; juveniles/younger cohort: r_s=0.036, N=7, P=0.905; subadults/younger cohort: r_s=0.452, N=8, P=0.233).

The mean percentage difference in size between the study litter and the two adjacent cohorts lessened as the animals aged (ANOVA: older cohort: F_3=117.29, P<0.001: younger cohort: F_2=12.154, P<0.001; Fig. 7.3) but this reduction in size disparity did not automatically lead to an increase in play. Study animals did increase the proportion of play bouts that they shared with members of the younger cohort (Fig. 7.3a), and by the age of 9-12 months, study animals were equally as likely to play with a member of the younger cohort as with a littermate (paired t test: t_6=0.140, P=0.893). However, study animals did not increase play with members of the older cohort as they grew (Fig. 7.3b), and there was no significant difference, between the pup and subadult periods, in the mean proportion of play bouts that they shared with a member of this cohort (paired t test: t_7=0.896, P=0.400) even though mean difference in weight dropped from 97% to 11% over this time (t_7=13.141, P<0.001).

7.4.2 Are play partners matched for ability?

Young meerkats did prefer play partners that were well matched in play fighting ability, and there was a negative relationship between the level of disparity in the outcome of a dyad's play wrestling bouts and degree of preference. Although this relationship was observed in all age classes (Fig. 7.4), it was at its strongest among pups, where disparity in winning play wrestling bouts accounted for 11% of the variation observed in partner preference.

Figure 7.2. Play partner preference as a function of percent difference in weight, for littermate dyads. (a) Pups; (b) juveniles; (c) subadults (Spearman rank correlation: pups: r_s= -0.34, N=104, P<0.000; juveniles: r_s= -0.276, N=122, P=0.002; subadults: r_s= -0.061, N=115, P=0.517).

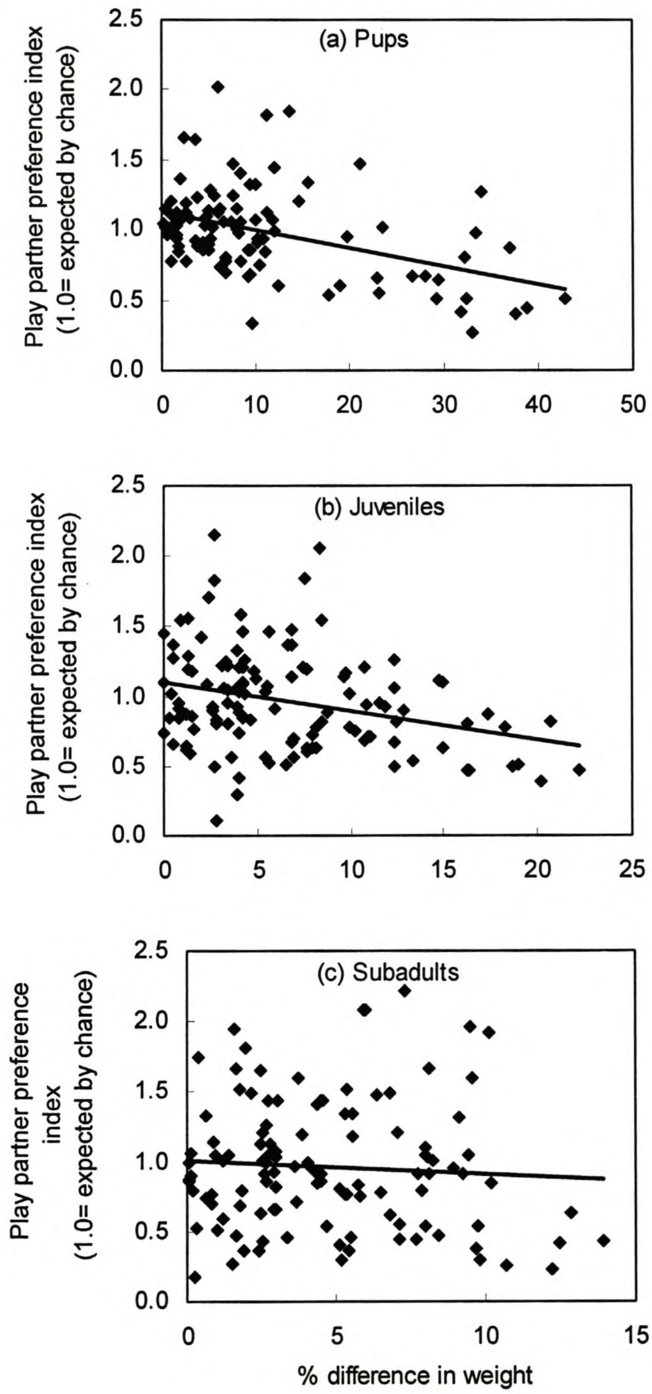


Figure 7.3. Mean weight difference between cohort and study litter, and mean percentage of play bouts shared with the average member of cohort, for (a) the adjacent younger cohort (*N*= 7 litters) and (b) the adjacent older cohort (*N*=9), by age of study litter.

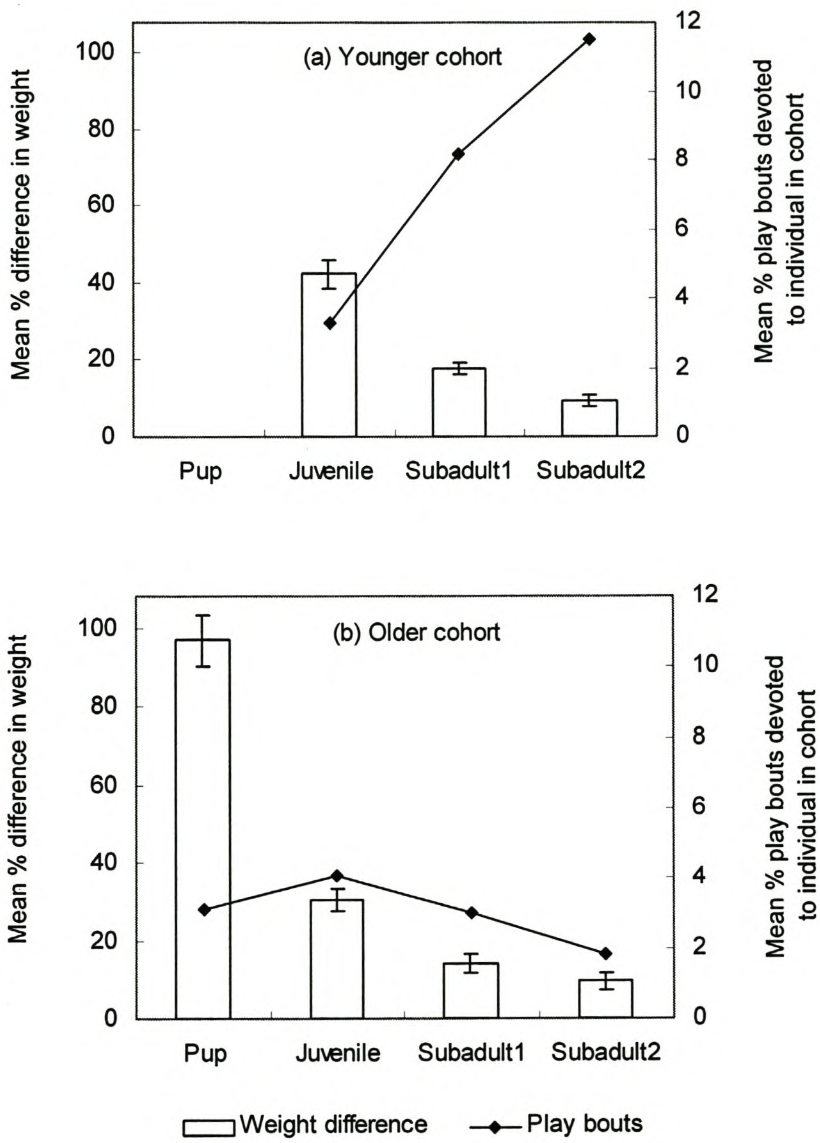
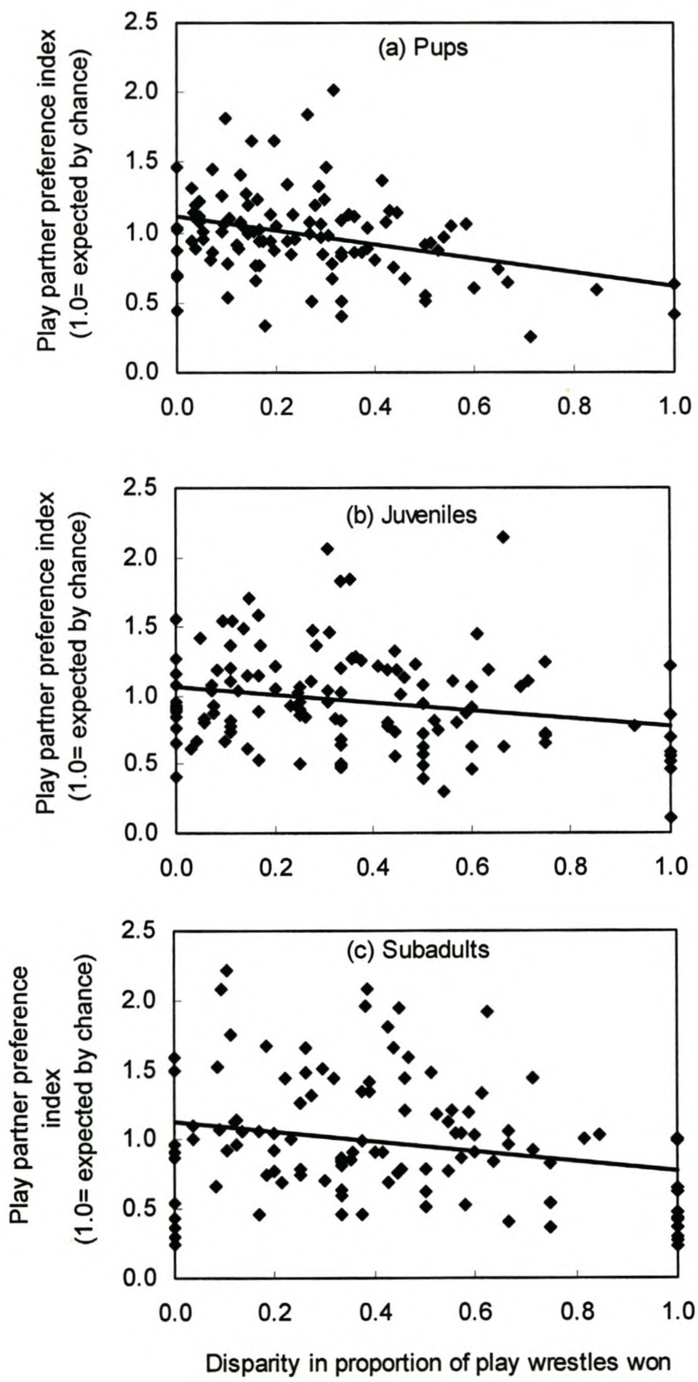


Figure 7.4. Play partner preference as a function of disparity in winning play wrestling bouts for dyads of littermates as (a) pups, (b) juveniles and (c) subadults (Spearman rank correlation: pups: r_s=-0.272, N=104, P=0.005; juveniles: r_s=-0.200, N=121, P=0.028; subadults: r_s=-0.193, N=112, P=0.042).



7.4.3 Do play partner preferences remain stable across development?

Dyads of littermates tended to maintain their level of play partner preference throughout their first 12 months of life (Spearman rank correlation: pup/juvenile: r_s=0.382, N=101, P<0.001; juvenile/subadult: r_s=0.374, N=115, P<0.001). However, a study animal's favourite play partner (always a littermate) rarely remained the same throughout its development. Less than one-third of study animals favoured the same littermate during both the pup and juvenile periods (regardless of whether preference was measured as the number of play initiations directed toward a littermate, or as the number of play bouts shared with a littermate), and only 7% of study animals consistently maintained the same favourite partner from the pup to subadult periods.

7.4.4 Do meerkats change play partners in response to changes in matching?

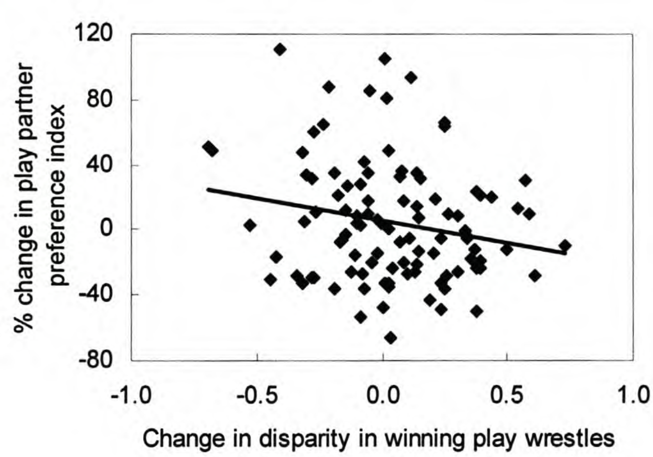
The win/lose disparities exhibited by littermate dyads during play wrestling bouts did not remain constant from the pup to juvenile period (Pearson correlation: r_{99}=0.148, P=0.140) and these changes in relative wrestling success were reflected in corresponding changes in play partner preference, with a negative correlation between change in level of disparity in winning play wrestling bouts (from the pup to juvenile periods) and percentage change in play partner preference index (Fig. 7.5). Between the juvenile and subadult periods, the win/lose disparities shown by dyads during play wrestling bouts tended to be maintained (r_{109}=0.271, P=0.004), and those changes that did occur were not correlated with shifts in play partner preference (Spearman rank correlation: r_s= -0.123, N=111, P=0.198).

Dyads that exhibited the greatest shifts in disparity in wrestling success from one age period to the next, showed no significant change in preference. Littermates that were initially closely matched for ability (i.e. each individual won at least 45% of their shared wrestling bouts) but whose abilities diverged in the following age period (with one individual winning more than two-thirds of their bouts) did not reduce their level of preference during the later age period (paired t test: pup/juvenile: t_{10}=0.049, P=0.962; juvenile/subadult: t_{11}=0.681, P=0.510). Similarly, dyads that were initially mismatched for ability but became evenly matched in the subsequent age period did not show an increase in preference (pup/juvenile: t_9=0.803, P=0.443; juvenile/subadult: t_9= -0.854, P=0.415).

Changes in size disparity also had only a minimal effect on preference. Members of a litter almost always maintained their weight differences throughout the course of development (Spearman rank correlation: pup/juvenile: r_s=0.913, N=101, P<0.001;

juvenile/subadult: r_s=0.864, N=115, P<0.001), but percentage differences decreased as the animals grew larger (dyads of pups averaged a 10.8 +/- 1.0% difference in weight, juveniles 6.6 +/- 0.5% and subadults 4.7 +/- 0.3%; Kruskal-Wallis: H_2=6.44, P=0.04). In littermate dyads, there was no correlation between the degree of change in weight disparity from one age period to the next, and percentage change in partner preference index (Spearman rank correlation: pup/juvenile: r_s= -0.121, N=101, P=0.228; juvenile/subadult: r_s= -0.001, N=115, P=0.995). However, dyads that showed the greatest reduction in weight disparity from the pup to juvenile periods (i.e. percentage weight difference fell by at least ten percentage points) showed a significant increase in preference (paired t test: t_{17}= -2.645, P=0.017). This trend was not observed in the transition from juvenile to subadult periods, and dyads with increasing levels of weight disparity showed no reduction in preference, at any age.

Figure 7.5. Percentage change in play partner preference index as a function of change in disparity in winning play wrestling bouts, in littermate dyads, between the pup and juvenile periods (Pearson correlation: r_{99}= -0.206, P=0.039).

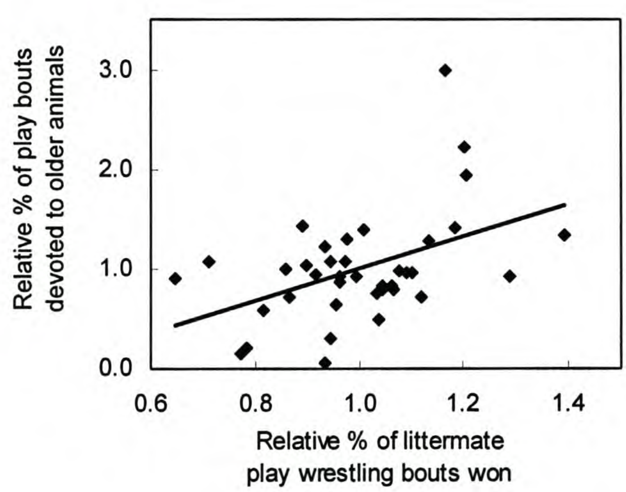


7.4.5 Do successful play fighters seek partners of increasing difficulty?

In meerkat pups, there was a positive correlation between the proportion of wrestling bouts an individual won during play with its littermates and the percentage of its play interactions that it devoted to older group members (both variables standardized by dividing by the mean value for same-sexed littermates; Fig. 7.6) suggesting that individuals capable of defeating their peers sought the greater challenge offered by older, and larger, siblings.

However, this relationship was not observed in juveniles or subadults (juveniles: Pearson correlation: r_{36}=0.008, P=0.961; subadults: Spearman rank correlation: r_s=0.217, N=43, P=0.162), and the relative degree of preference for older playmates that an individual adopted as a pup was consistently maintained through to adulthood (Spearman rank correlation: pup/juvenile: r_s=0.845, N=38, P<0.001; juvenile/subadult: r_s=0.728, N=43, P<0.001) regardless of later wrestling success. An individual's relative preference for play with younger group members (only available to juvenile and subadult meerkats) was unrelated to relative wrestling success with littermates.

Figure 7.6. Percentage of play bouts that pups shared with older group members as a function of success during play wrestling with littermates (both variables expressed as deviations from same-sex litter mean – i.e. a value of 1.0 equals the mean; Spearman rank correlation: r_s=0.372, N=38, P=0.022).



7.4.6 Which animals initiate play more frequently?

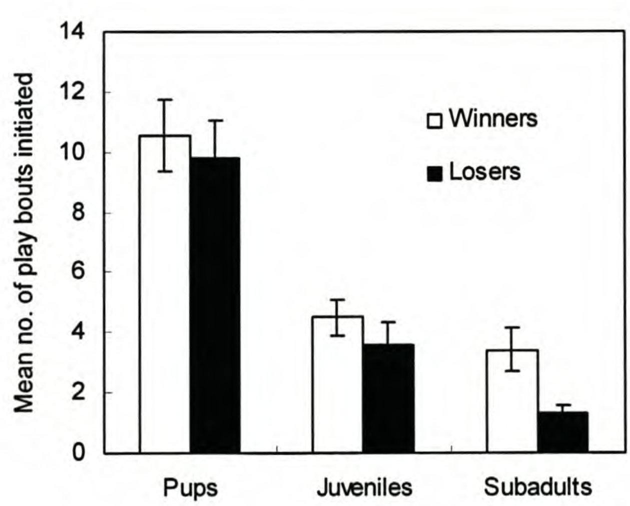
In littermate dyads, disparity in play initiations increased with age, rising from an average of 20.0 +/- 1.5% in pups to 34.2 +/- 2.7% in juveniles and 53.1 +/- 3.5% in subadults (Kruskal-Wallis: H_2=48.185, P<0.001).

Size difference between the members of a dyad did not influence which animal was most likely to initiate the pair's play bouts, with no correlation between percentage weight difference (directional) and proportion of play bouts initiated, at any age (Spearman rank correlation: pups: r_s= -0.124, N=104, P=0.211; juveniles: r_s=0.051, N=110, P=0.595; subadults: r_s=0.025, N=111, P=0.791). Even in dyads that were severely mismatched for size (top 20% of littermate dyads, with a mean weight difference of 30% for pups, 16% for juveniles and 10% for subadults), the smaller individual initiated just as many play bouts as the larger animal (paired *t* test: pups: t_{19}= -0.302, *P*=0.766; juveniles: t_{19}=0.547, *P*=0.59; subadults: t_{19}=0.229, *P*=0.821).

The likelihood of initiating play, among littermate dyads, was also unrelated to level of play fighting success, with no relationship between directional disparity in success (wrestling or chasing) and directional disparity in play initiations, at any age. Littermate dyads that were severely mismatched for play wrestling success (top 20%, with a mean disparity of 0.59 for pups, 0.70 for juveniles and 0.84 for subadults), behaved in a similar manner during the pup and juvenile periods, but as subadults, the winning individual initiated significantly more of the pair's play bouts than the loser (Fig. 7.7).

Level of success during play wrestling in one age period was also unrelated to the relative likelihood of initiating play with that partner during the next age period for opposite-sexed dyads (Pearson correlation: pup/juvenile: r_{51}= -0.087, *P*=0.536; juvenile/subadult: r_{57}=0.089, *P*=0.500) but in same-sexed dyads the winner was more likely than the loser to initiate the pair's play interactions during the subsequent age period (pup/juvenile: r_{45}=0.335, *P*=0.021; juvenile/subadult: Spearman rank correlation: r_s=0.330, *N*=51, *P*=0.018).

Figure 7.7. Mean number of play bouts initiated by the winning individual versus the losing individual in littermate dyads that showed severe disparity in play wrestling success (Wilcoxon signed rank test: pups: *W*=-30.000, *N*=20; *P*=0.487; juveniles: *W*=-64.000, *N*=20; *P*=0.105; subadults: *W*=-120.000, *N*=20; *P*=0.007). Vertical lines indicate SE.



7.5 DISCUSSION

The predictions generated by the self-assessment hypothesis were at least partially fulfilled by the behaviour of young meerkats. Meerkats strongly preferred to play with partners matched for age (Fig. 4.1) and this is consistent with observations for many other taxa (e.g. ungulates: Berger 1980; Byers 1980; Pfeifer 1985; Gormendio 1988; Rothstein & Griswold 1991; Hass & Jenni 1993; Thompson 1996; primates: Cheney 1978; Symons 1978b; Stevenson & Poole 1982; Boulton 1991; Govindarajula et al. 1993; Mendoza-Granados & Sommer 1995; and a macropod: Watson 1993). Although it is generally assumed that preference for same-aged partners is a result of individuals attempting to minimize disparity in size (Thompson 1996), this study is the first to demonstrate that disparity in both size (measured as percentage weight difference) and ability (measured as relative success during play wrestling) were negatively correlated with partner preference in same-aged animals (Fig. 7.2; Fig. 7.4). However, this was only the case during the peak period of social play in meerkats (prior to 6 months of age; Fig. 6.1). In older animals (6-12 months of age) disparity in ability was only weakly related to partner choice (accounting for 4% of the variation observed in partner preference) and size disparity was unrelated to partner choice. Although this is potentially explained by the relatively low percentage weight differences (always less than 15%) that existed between littermates of this age, this does not account for the reduced effect of disparity in ability. Clearly, additional factors were influencing partner choice in subadults, and these were most likely to be related to the animals' developing awareness of social status (Fig. 8.3).

Thompson (1998) suggests that play between partners at the same stage of development should be favoured, not only because such animals will be well-matched and hence provide the most precise feedback, but because this allows individuals to monitor the efficacy of their own development relative to that of others. She argues that the best way to obtain this information is to play consistently with one well-matched, same-aged partner throughout the course of development (prediction number two). Meerkats, however, only partially fulfilled this prediction, for although individuals generally maintained their partner preferences up to adulthood, they did not show a strong, consistent preference for one particular partner, as Thompson (1996) observed in sable antelope, *Hippotragus niger*. However, in species bearing litters (rather than single offspring), across-litter comparisons would provide a more reliable measure of normal development than fidelity to a single peer.

It is difficult to discern whether the meerkats' preference for littermates was due solely to the benefits of size matching or whether they were also using play to monitor self-development. Although the proportion of play bouts dedicated to littermates decreased with age (Fig. 4.1) concurrent with a reduction in percentage size difference between study animals and other group members (and study animals actually favoured their younger siblings as strongly as littermates by 9-12 months of age, after mean weight differences had fallen to 9%), reductions in size disparity did not inevitably lead to an increase in play (Fig. 7.3). Similarly, study litters in which the adjacent cohort was close in size to the study litter (due to fluctuations in food availability), were no more likely to play with these nonlittermates than study litters in which the gap was wide. Qualitative observations suggest that animals whose growth has been severely stunted, by congenital defect or disease, still prefer to play with littermates, even though they are grossly mismatched for size, and well-matched partners from younger cohorts are available. Similarly, full-grown meerkats (2-3 years old) still prefer littermates and this predilection seems to persist throughout life if the opportunity exists. Several researchers (Berger 1980; Markus & Croft 1995; Spinka et al. 2001) have suggested that animals prefer playing with close relatives (such as littermates) because they are most familiar with these individuals, but this seems a less credible explanation in a species that lives in very tightly-knit groups, in which all members are intimately associated and closely related.

The third prediction arising from the self-assessment hypothesis (that both members of unevenly matched dyads will be equally disinterested in playing) is of particular importance because it allows us to distinguish between the self-assessment hypothesis and two alternative explanations. The first of these, is that animals choose to play with well-matched peers because they are using play to contest status or assert dominance (Carpenter 1934; Dolhinow 1971; Poirier & Smith 1974; Geist 1978; Symons 1978a, Berman 1982; Paquette 1994; Chapter 9), and the second explanation proposes that individuals are simply trying to maximize their chances of winning play fights so as to accrue the psychological benefits of success (e.g. increased confidence; Sutton-Smith 1993, 1995; Biben 1998). In both of these cases, losers in unevenly matched dyads would be expected to initiate play less often than winners, and such patterns of initiation have been observed in a variety of species (Owens 1975a; Symons 1978; Byers 1980; Hole 1988; Boulton 1991; Biben 1998). In meerkats, however, there was no difference in the frequency of initiations made by either member of unevenly matched littermate dyads, regardless of whether they were mismatched for size or play fighting ability. There were, however, two exceptions to this general finding. Firstly, among subadult littermates that were severely mismatched for wrestling success, winners initiated play more frequently than losers. This is consistent with the tenet that issues of social status increasingly influenced play as meerkats approached adulthood (Chapter 9). That the change in initiation patterns was related to status, rather than the need to avoid the psychological hazards of losing (Sutton-Smith & Kelly-Byrne 1984), is confirmed by the fact that dyads of same-sexed littermates behaved differently from dyads of opposite-sexed littermates, even though meerkats show no sexual dimorphism in size (Clutton-Brock et al. 2002), or in frequency (Fig. 6.2), or behavioural content (Section 9.4.3), of play. Level of wrestling success during one age period was positively related to the likelihood of initiating play with that partner during the next age period in same-sexed dyads, but not in opposite-sexed dyads. This apparent aversion to losing to same-sexed peers is readily explained by the fact that status-related agonistic interactions are directed primarily toward same-sexed littermates (Chapter 8).

A different pattern of initiations was observed when meerkats of different ages played together, with young (smaller) animals initiating play more frequently than their elders (Chapter 4). The disparity in initiations increased with increasing difference in age (and thus size), with younger animals responsible for 70% of the play initiations that occurred between individuals more than 5 months different in age (L. Sharpe, unpublished). Age-dependent variation in frequency of play can only partially explain this trend (Chapter 4), which is similar to that observed in Cuvier's gazelles, *Gazella cuvieri* (Gomendio 1988). Although, contrary to the prediction generated by the self-assessment hypothesis, this trend is not entirely incompatible with the theory, because older individuals will gain little useful feedback from play with very small, weak partners, but growing youngsters are likely to learn much about their own developing abilities from the occasional play bout with a large, well-grown partner. The pattern of initiations observed in partners of different age is also consistent with the 'training for the unexpected' hypothesis (Spinka et al. 2001) which asserts that play teaches animals how to cope with sudden, unexpected loss of control (e.g. falls, defeat), and thus individuals seek out play opportunities which provide temporary loss of control, such as play with partners that can defeat them. This hypothesis, however, fails to explain why meerkats show a marked preference for play partners that are closely matched for age, size and ability.

One of the key predictions arising from the self-assessment hypotheses is that if the degree of disparity between play partners undergoes a change, preference for that partnership will alter accordingly (prediction number four). This study, the first to test the prediction, found little evidence in support. In youngsters under 6 months of age, change in disparity in ability (wrestling success) within littermate dyads was negatively correlated with change in partner preference, but the relationship was weak, with shifts in disparity accounting for only 4% of the change seen in preference (Fig. 7.5). Dyads that experienced large changes in disparity in ability did not respond with a change in preference, and shifts in size disparity had no effect on partner choice, except in dyads that experienced an extreme reduction in disparity. These findings suggest that the minimization of disparity, although of importance to meerkats less than 6 months of age, was not the most influential factor determining the choice of play partners. In older animals (juveniles/subadults) changes in disparity were unrelated to partner choice, and this is consistent with the assertion that social factors were impinging on partner choice in this age group (Chapter 9).

The final prediction examined in this study springs from Thompson's (1998) assertion that play is progressive, and individuals which have mastered one 'play task' will progress to more difficult play challenges. Meerkat pups do appear to conform to this prediction, with a positive correlation between level of success during play with peers, and frequency of play with more challenging partners (i.e. older group members that are larger and more experienced). However, this relationship was not found in juvenile or subadult meerkats, which generally maintained the play partnerships they established in infancy. This finding is not necessarily inconsistent with Thompson's concept of progressiveness, since social play normally involves developing individuals whose strength and skill increase with time. However, if play brought about a progressive improvement in performance, as assumed by the theory, meerkats that played more frequently than their peers should, over time, show a greater degree of improvement in play fighting ability than those that played infrequently, and this was not the case (Chapter 6). Similarly, unsuccessful play fighters did not devote more time to play (Chapter 6) as would be anticipated if the feedback obtained from play was used by an individual to 'modify its play for optimal benefit' as proposed by Thompson (1998, pp. 199).

Another problem facing the self-assessment hypothesis is the occurrence of social play in which players do not exert their full capabilities. For example, self-handicapping - in which the stronger partner does not play to full capacity (Watson & Croft 1996; Pereira & Preisser 1998; Spinka 2001) - makes it impossible for animals to accurately gauge their own abilities. Although play fighting success in meerkat pups does appear to reflect actual competitive ability (Fig. 7.1), and self-handicapping is probably not prevalent in this species (Chapter 6), a sizeable component of meerkat play does take place at sub maximal levels of intensity.

During the midday rest period, for example, youngsters normally spend much time lying together in the shade, gently batting at one another and mouthing one another's extremities. Such low-intensity play is valueless in terms of self-assessment.

Although the behaviour of meerkats under 6 months of age did tend to fulfill the predictions generated by the self-assessment hypothesis, and youngsters certainly favoured play with well-matched partners, neither the patterns of partner choice or the structure of meerkat play made play optimal for the purposes of self-assessment. There was nothing to suggest that the feedback meerkats obtained from play was used to modulate their own play behaviour or their physical development, although, of course, the study did not set out to test these assertions. Young meerkats also did not appear to modify their behaviour toward playmates in response to the potential feedback on relative abilities provided by play. For example, play wrestling success was unrelated to the likelihood of initiating aggressive interactions in pups competing for food (L. Sharpe, unpublished), or to the likelihood of initiating competitive dominance interactions with same-sexed peers (Chapter 9). However, there is some evidence that the information gained in play may be used cognitively (i.e. applied in other contexts) because meerkats that routinely lost play fights with their peers differed in their behaviour towards older group members (with which they rarely played) and dispersed at different times from littermates that routinely won play fights (Chapter 9). Although this finding is consistent with the assertion that competitive social play assists in the evaluation of social risk (Thompson 1998; Spinka et al. 2001), the causality of this relationship is virtually impossible to ascertain in the field.

CHAPTER EIGHT

DOMINANCE RELATIONSHIPS IN THE MEERKAT (*SURICATA SURICATTA*)

8.1 ABSTRACT

Although the meerkat, *Suricata suricatta*, is a relatively well-studied species, little is known of the social structure of its groups, apart from the obvious social ascendancy of the dominant breeding pair. This study documented the status-related agonistic behaviour of young meerkats living in their natal group in a wild population in the southern Kalahari Desert. The study found that the group's alpha female elicited the majority of the submissive behaviour exhibited by subadult animals of both sexes, although young females submitted to the alpha female ten times more frequently than did their male counterparts, confirming the alpha female's control over subordinate female reproduction and emigration. Although overt displays of aggression and submission between non-dominant group members were rare, it appeared that older animals were socially dominant to younger animals, and females dominant to males. Rates of agonism in subordinate females were also considerably higher than in males. Competitive agonistic interactions (in which dominance was mutually contested by both interactants) were far more prevalent than directional interactions. Competition was primarily intrasexual, occurring most frequently between same-sexed littermates (animals most likely to disperse together), and although individuals with a competitive advantage (in size, age or sex) were more likely to initiate competitive interactions, such interactions appeared to be used to convey information about the strength and motivation of contestants, rather being a means of attaining social dominance within the natal group, and meerkats willing dispersed with active competitors even though they avoided dispersing with individuals with which they had shared directional dominance interactions.

8.2 INTRODUCTION

Meerkats, *Suricata suricatta*, are diurnal, terrestrial, insectivorous mongooses that are highly gregarious. Along with the other members of the social mongoose group (subfamily Mungotinae, within the family Herpestidae; Wozencraft 1989), they are renown for the complexity of their social behaviour, and their highly developed cooperative behaviour has attracted much research (e.g. Clutton-Brock et al.1998, 1999, 2000, 2001, 2002; Doolan & MacDonald 1999; Brotherton et al. 2001; Russell et al. 2002, 2003b). Despite this, however, very little is known about the internal social structure of meerkat groups. A number of studies have assessed the degree of control that the group's alpha pair exerts over the reproduction of subordinates (Doolan & MacDonald 1997b; O'Riain et al. 2000; Clutton-Brock et al. 2001c; Griffin et al. 2003; Carlson et al. in prep.), but the social relations existing among non-dominant group members are not known. It is also not known whether meerkats exhibit sexual dimorphism in agonistic behaviour. In most mammals, males exhibit higher frequencies of agonism than females and this is attributed to the polygyny of mammalian mating systems (in which successful males can reap far greater reproductive rewards than females; Clutton-Brock et al. 1982). However, cooperatively breeding meerkats show equally high reproductive skew in both sexes (Clutton-Brock et al. 2001b), and hence the sexes might be expected to invest equally in agonistic behaviour.

To answer these questions, this study examines the agonistic behaviour of young meerkats living in their natal group, in a wild population located in the southern Kalahari Desert. Meerkats are obligate cooperative breeders (Clutton-Brock et al. 2001b) whose groups are normally comprised of 3-40 individuals, consisting of a dominant breeding pair, the pair's offspring (which, despite attaining sexual maturity at 7-11 months of age, delay dispersal until around 2 years of age; Chapter 5) and several immigrant males (Clutton-Brock et al. 2001b). The group's alpha pair enjoys social ascendancy over all other group members (Clutton-Brock et al. 1998a; Gsell 2002) and successfully monopolizes 75% of the group's total reproductive effort (Griffin et al. 2003). The alpha female also forcibly expels subordinate females from the group (during the later stages of her own pregnancy), with subordinates often suffering several short-term evictions before actually emigrating (Clutton-Brock et al. 1998a). Young males appear to disperse from their natal group voluntarily, after undertaking repeated short-term prospecting forays to neighbouring groups (Doolan & MacDonald 1996b). Both sexes usually disperse in the company of same-sexed group members (most commonly littermates; Chapter 4), and ultimately fight these co-dispersers for the dominant position within a newly founded group (Chapter 6).

This study documents the status-related agonistic behaviour of natal meerkats to determine: (1) whether the control attributed to the group's alpha pair by reproductive studies is confirmed behaviourally; (2) whether non-dominant group members exhibit a dominance hierarchy; and (3) whether the sexes differ in their agonistic behaviour across development.

8.3 METHODS

I carried out the study between August 1999 and September 2003, working on a natural population of meerkats living on ranchland in the southern Kalahari Desert, 30 km west of Van Zylsrus, South Africa (26°58'S, 21°49'E). See Section 1.6 for details of the study site's topography, vegetation and rainfall. The work was carried out under licenses issued by the Northern Cape Conservation Service, South Africa. All meerkats in the study were habituated to close observation and handling, and were individually marked with permanent marker pen on the tail, plus a small patch of snipped fur on the body (both applied unobtrusively while the animals were sunning at the burrow). All study animals were monitored several times a week, from birth until they dispersed from their natal group, died or attained at least 36 months of age. All dispersing individuals were observed after they left their natal group and most were followed until they established or joined another group.

The body weight of study animals was measured by enticing them, with a crumb (<0.5g) of hard-boiled egg, to stand on an electronic balance. The meerkats were generally weighed three times a week, first thing in the morning, before they left the burrow to forage. To ascertain an individual's mean subadult weight, I averaged the animal's weight measurements on a 2-weekly basis, and then averaged these 13 bi-weekly means. To calculate weight difference between same-sexed littermates, I expressed the difference between the two individuals' mean bi-weekly weights as a percentage of the pair's mean weight, and then averaged these 13 percentage differences to generate a value for the subadult period.

I collected data on agonistic interactions for eight litters of meerkats (42 individuals) from six groups, throughout their first 12 months of life. Additional data were collected for one litter (seven individuals) during the juvenile and subadult periods only. Two of the study litters were comprised of pups borne by more than one female, but the youngsters (within 2 weeks in age) were raised together as a single litter, and were treated as such in this analysis.

I documented agonistic interactions ad libitum (Altmann 1974), whenever an interaction involving a study animal was observed. For each interaction, I recorded the identity and behaviour of the participants (as described below), and noted which individual initiated the interaction (if this was clear). Aggressive interactions over food were not included, as these were almost inevitably won by the original owner of the food item (Barnard 2000), and revealed little about dominance status. In total, I documented 917 status-related agonistic interactions, with an average of 102 per study litter.

Aggressive status-related behaviour (also referred to as assertions of dominance) consisted of one or more of the following behaviours:

glare - crouches and fixes other animal with an unwavering stare;

approach - marches purposefully toward the other animal while glaring at it;

charge - charges directly at the other animal;

hip-slam - slams side of body against the other animal;

chin mark - rubs sub maxillary gland (Gsell 2002) rapidly back and forth on the other animal's head or body;

head shake - a gesture similar to a chin mark, but without physical contact;

hit - swats other animal with one paw;

sit-on - sits down on other animal's head (when victim is crouching or lying on its back)

attack - bites other animal, often repeatedly.

Submissive status-related behaviour consisted of one or more of the following behaviours:

avoid – slinks away, or changes direction of movement, to avoid aggressor;

submission call – crouches down and emits a high-pitched, peeping vocalization (Manser 1998);

roll over – rolls over and lies on back, in a semi-curled posture;

flee – runs away.

Subordinate animals sometimes initiated interactions, approaching the higher-ranking animal slowly, at a crouch, while giving continuous submission calls. The subordinate animal sometimes went on to groom the dominant individual, while continuing to call.

Agonistic interactions were classified as 'directional' when one interactant behaved aggressively and the other behaved submissively, regardless of which animal initiated the interaction. Interactions in which both participants behaved aggressively toward one another were classified as 'competitive'. These interactions normally consisted of mutual, synchronous hip-slamming or head shaking, but mutual chin marking and synchronous *rearing* (an escalated hip-slam in which both animals rise up bipedally, pushing against one another's shoulders) did also occur. Aggressive behaviour that was not reciprocated in any way (i.e. it was ignored by the recipient) did occasionally occur, but these interactions were excluded from the analysis because they generally did not reflect a relationship between the participants. For example, a meerkat watching the approach of a rival may ostentatiously hip-slam the animal standing next to it, but the recipient simply ignored the threat because it was clear that the perpetrator was concentrating its attention upon another animal.

As with most kinds of social behaviour in meerkats, dominance-related interactions occurred almost exclusively when group members were gathered together at a burrow entrance. To ascertain hourly rates of interactions, I limited the analysis to the period the group spent at the burrow in the morning before setting off to forage (a total of 248 hours of data collection, or 27.6 hours per study litter). To compare the rates of interaction observed in my study animals with those shown by adults, I collected supplementary data on agonistic interactions for 19 adult meerkats (aged 14-29 months; mean 19.9 +/- 0.8 months) living within their natal groups. I obtained an average of 18.9 hours of data (at the morning burrow) for each of these animals (11 males and eight females, from six litters in three groups) over a 10-week period (May-July).

When assessing which group members the study animals interacted with, I limited the analysis to data collected during the subadult period only (as younger animals interacted too infrequently) and included all documented agonistic interactions, regardless of when or where they occurred. The rarity of status-related agonistic interactions among meerkats in their natal group prohibited the detailed analysis of relationships between individual group members, so I used age/sex categories, employing the following age categories: pup, less than 3 months old; juvenile, 3-6 months old; subadult, 6-12 months old; and adult, over 12 months old. In all calculations of group size, or the age/sex composition of a group, I adjusted for any temporary absences of group members. The study groups did not show any sex ratio bias (paired t test: t_8= -1.966, P=0.85) with females averaging 46.9 +/-1.4% of group members.

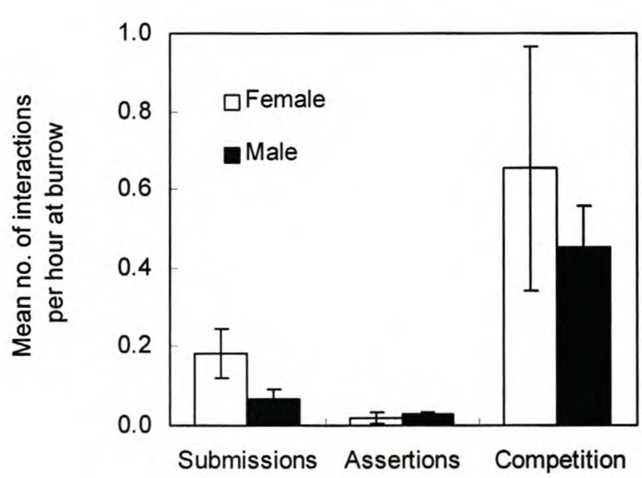
To standardize individual data derived from different litters I used 'deviation from same-sex litter mean'. To obtain this measure, I divided the value for each individual by the mean value for that sex in its litter (hence a value of one equals the mean). Animals that were their litter's sole representative of a sex were excluded from these analyses. I chose this method of standardization because it corrects for factors that affect the mean (e.g. litter size, group size and composition, territory quality, season, etc.) but maintains interlitter differences in variance (caused primarily by individual differences between littermates). All references to 'relative' values refer to deviations from same-sex litter mean. I used parametric statistical tests throughout the analysis, except where the data differed significantly from a normal distribution (based on the Kolmogorov-Smirnov test for normality), in which case I used equivalent nonparametric tests. All statistical tests were two-tailed with a significance threshold of 0.05. Means are given +/- SE.

8.4 RESULTS

8.4.1 Frequency of agonistic interactions

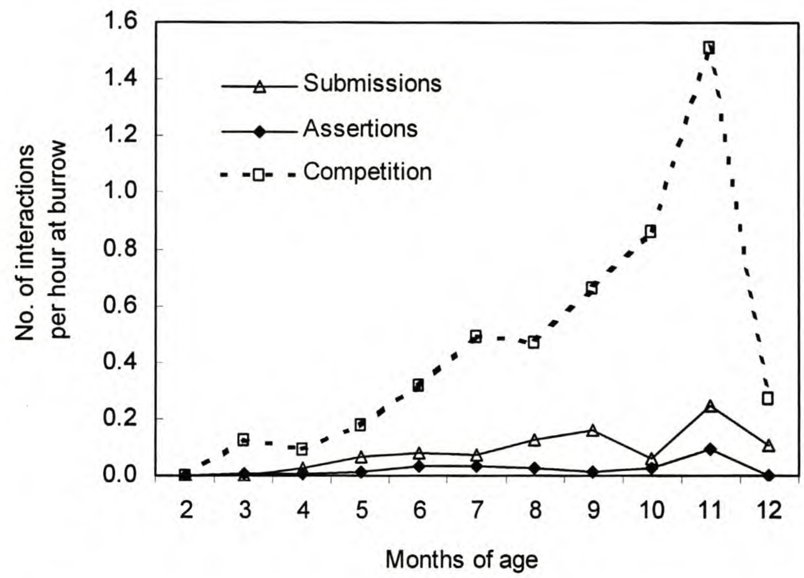
Directional dominance interactions (in which one animal asserted its dominance and the other behaved submissively) occurred relatively infrequently in natal meerkats. On average, subadult meerkats submitted to another group member 0.12 +/- 0.05 times per hour, and asserted their dominance over other animals 0.03 +/-0.01 times per hour. Competitive dominance interactions (in which both interactants attempted to assert dominance over the other) occurred four times more often than directional interactions (Fig. 8.1) with the average subadult meerkat competing 0.65 +/-0.21 times per hour. There was a positive correlation between how frequently a subadult indulged in competitive interactions and how frequently it behaved submissively (both variables measured relative to same-sexed littermates; Pearson correlation: r_{39}=0.320, P=0.042).

Figure 8.1. Mean frequency of status-related agonistic interactions in subadult meerkats, by sex (paired t test: submissions: t_8=3.155, P=0.013; assertions: t_8=0.083, P=0.936; competition: t_8=1.285, P=0.235). See Section 8.3 for definitions. Vertical lines indicate SE.



The age distribution of dominance-related behaviour, in meerkats under 12 months of age, is shown in Figure 8.2. Adult meerkats, living in their natal group, were involved in almost twice as many directional dominance interactions as subadults (undertaking 0.22 +/- 0.04 submissions per hour and 0.06 +/- 0.02 assertions per hour), but they showed a similar rate of dominance competition, undertaking 0.65 +/- 0.14 competitive interactions per hour.

Figure 8.2. Mean frequency of dominance-related agonistic interactions by age (*N*=9 litters). See Section 8.3 for definitions.

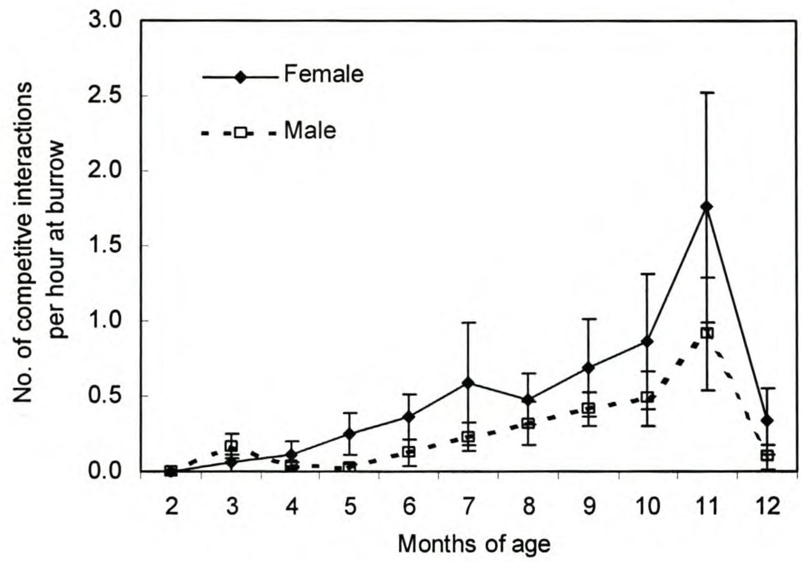


8.4.2 Sex differences

Female subadults were involved in three times as many submissive interactions as males with the average subadult female submitting to another meerkat once every 5 hours, compared with once every 17 hours for a male (Fig. 8.1). This sex difference was maintained into adulthood, with adult natal females submitting 2.5 times as frequently as adult natal males. There was no difference between the sexes in the frequency with which subadults asserted their dominance over other group members (Fig. 8.1).

Subadult females were involved in a competitive interaction once every 1.5 hours at the burrow, compared with once every 2.2 hours for males (Fig. 8.1). This sex difference, although remaining consistent across development (Fig. 8.3) was not statistically significant when rates for males and females within a litter were compared (Fig. 8.1) because the frequency of competitive interactions in females was strongly positively correlated with the number of females in the litter (Fig. 8.4a). In contrast, rate of competition in males was unrelated to the number of same-sexed animals in the litter (Fig. 8.4b).

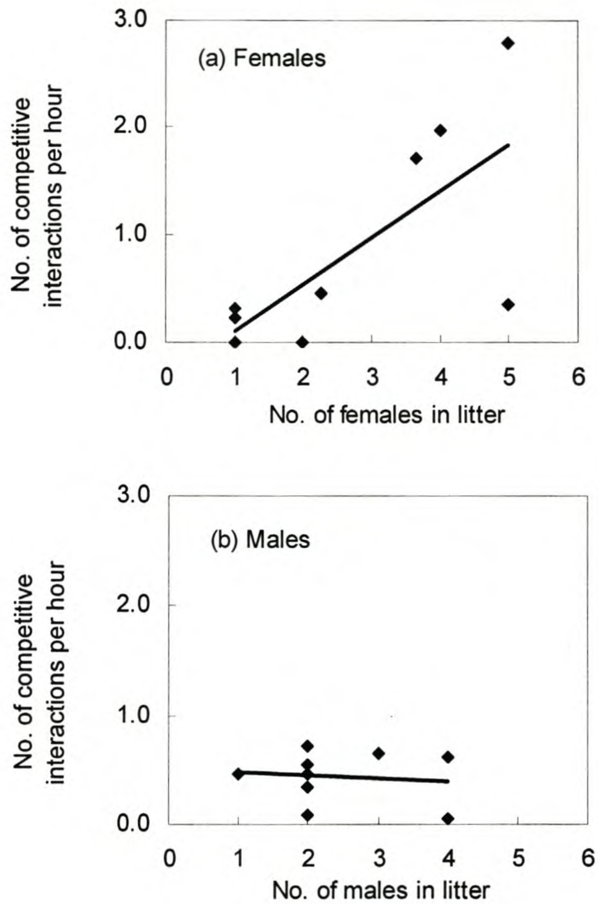
Figure 8.3. Mean frequency of competitive agonistic interactions by age and sex. Vertical lines indicate S.E.



8.4.3 Interactions with the dominant breeding pair

The group's dominant breeding pair, although comprising, on average, only 9% of all group members, was responsible for more than three-quarters of a subadult's submissive interactions. This figure was even higher for natal adults, which dedicated 85% of their submissions to the dominant pair. The alpha female appeared to wield a far greater influence than the alpha male, eliciting 76% of subadult females' submissive interactions and 62% of subadult males' (paired *t* test: t_8=1.718, P=0.124), while the dominant male induced 19% of male submissions and 4% of females' (t_8=3.274, P=0.011). Female subadults submitted to the group's dominant female almost ten times more frequently than did their male littermates, but the sexes did not differ in their frequency of submission to the dominant male (Fig. 8.5). Subadult meerkats never directed dominance assertions or competitive dominance behaviour toward the group's dominant breeding pair.

Figure 8.4. Mean frequency of competitive agonistic interactions in subadult meerkats as a function of number of same-sexed animals in litter: (a) females (Spearman rank correlation: r_s=0.769, N=9, P=0.012); and (b) males (r_s=0.028, N=9, P=0.913).



8.4.4 Interactions between non-dominant group members

Directional dominance interactions between non-dominant group members were rare, in fact the average natal meerkat (both subadult and adult) was involved in such an interaction only 0.08 times per hour at the burrow. Female subadults submitted to non-dominant group members twice as frequently as did their male counterparts, although this difference did not attain statistical significance (Wilcoxon signed-rank: W= -29.000, N=9, P=0.098). Older group members elicited 76.1 +/- 2.3% of a subadult's non-dominant submissions, which was significantly more than expected by chance (paired t test: t_8=4.566, P=0.002) since older animals comprised only 42.3 +/- 3.8% of the group's non-dominant members (Fig. 8.6).

Subadults submitted to younger group members much less often than was expected by chance (t_8= -6.281, P<0.001) with only 3.0 +/- 2.2% of their submissions elicited by this age class, which comprised 31.9 +/- 3.5% of the group. The frequency with which subadults submitted to same-aged animals (i.e. littermates) did not differ from that expected by chance (t_8= -6.08, P=0.560). Subadult meerkats undertook dominance assertions too rarely to allow any detailed analysis of this behaviour, but younger group members were targeted more frequently than other age classes (suffering 45% of a subadult's assertions; Fig. 8.6).

Competitive dominance interactions were directed primarily toward same-aged animals (Fig. 8.6), with littermates (which comprised 25.8 +/- 3.6% of the group's non-dominant members) involved in 72% of a subadult's competitive interactions (significantly more than expected by chance: paired t test: t_8=4.557, P=0.002). Subadults competed less often than expected with older non-dominant group members (t_8=5.871, P<0.001) and showed a similar, but non-significant, trend with younger group members (t_8=1.932, P=0.089; Fig. 8.6). When animals differing in age did compete, the older individual was much more likely than the younger animal to have initiated the interaction (t_8=2.348, P=0.047), with older animals initiating 82.7 +/-7.1% of these mixed-aged interactions.

During submissive interactions involving non-dominant group members, female subadults submitted to same-sexed animals almost three times as often as they submitted to opposite-sexed animals (paired t test: t_8=3.178, P=0.013), with 73.3 +/- 6.1% of their submissions directed toward female group members. In contrast, males were equally likely to submit to either sex of non-dominant animal (t_8= -0.324, P=0.754), with opposite-sexed animals eliciting 44.0 +/- 14.2% of their submissions. During competitive dominance interactions, both sexes favoured same-sexed group members, with subadult males directing 75.3 +/- 10.0% of their competitive interactions at same-sexed individuals, and females 79.2 +/- 7.8% (males: t_8=3.584, P=0.007; females: t_8=2.322, P=0.059). When opposite-sexed animals competed, the female was more likely than the male to have initiated the interaction (paired t test: t_8=2.475, P=0.038), with females initiating 71.7 +/- 13.6 % of all mixed-sexed competitive interactions.

Figure 8.5. Mean hourly rate of submissions directed toward older group members by subadult meerkats. (Difference between sexes: paired t test: dominant female: t_8=2.506, P=0.036; other female: t_8=1.702, P=0.127; Wilcoxon signed-rank: dominant male: W= -4.000, N=9, P=0.625; other male: W= 6.000, N=9, P= 0.250.) Vertical lines indicate SE.

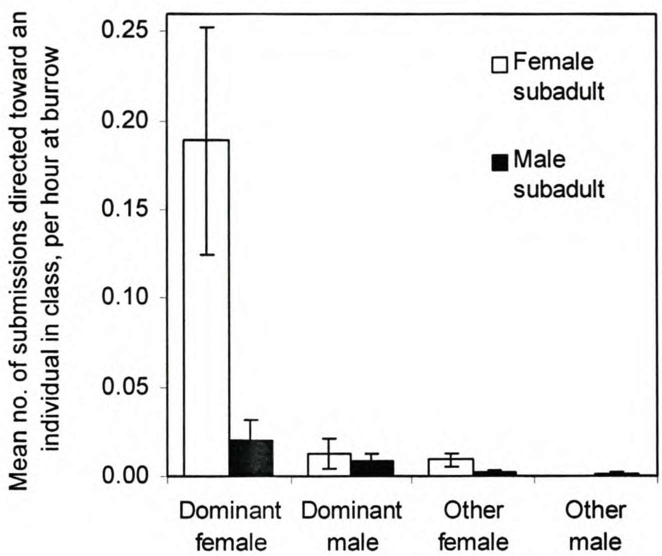
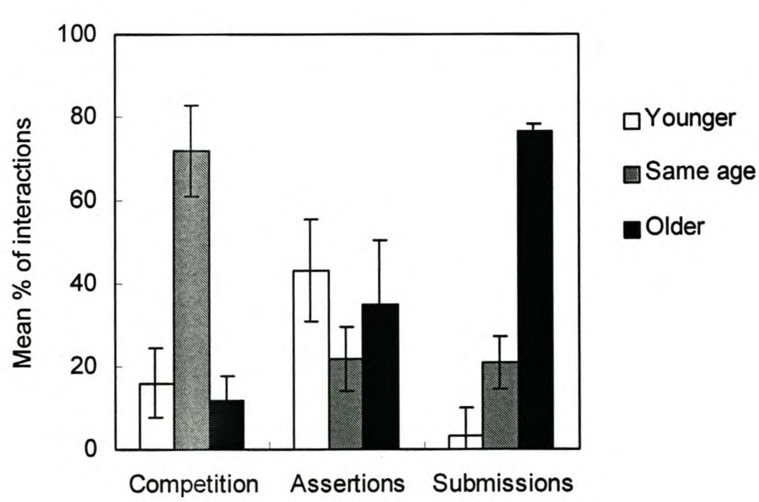


Figure 8.6. Status-related agonistic interactions between subadults and non-dominant group members, by age of interactant (N=9 litters). See Section 8.3 for definitions. Vertical lines indicate SE.



8.4.5 Body weight

There was no relationship between body weight and frequency of submissive interactions in subadult meerkats (both variables measured relative to same-sexed littermates; Pearson correlation: r_{39}=0.274, P=0.083), but relative weight was positively correlated with relative frequency of competitive interactions (r_{39}=0.430, P=0.006). Among same-sexed littermates, there was a positive correlation between percentage difference in weight (between the first and second member of the dyad) and the percentage difference in number of the competitive interactions initiated (i.e. animals that were larger than a same-sexed littermate tended to initiate a greater proportion of the pair's shared competitive interactions; Pearson correlation: r_{38}=0.357, P=0.024).

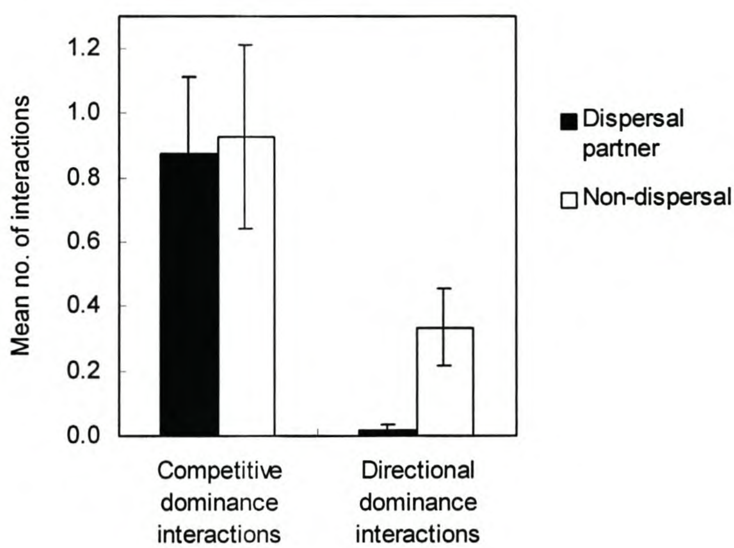
8.4.6 Prospecting, eviction and emigration

Males that submitted less frequently than their male littermates began undertaking prospecting forays (i.e. short term visits to neighbouring groups) earlier than those that submitted more frequently (Pearson correlation: r_{19}=0.581, P=0.006). It appeared to be submissions to the group's dominant female (r_{19}=0.482, P=0.027) that generated this relationship, as there was no correlation with submissions to the dominant male or same-sexed non-dominant group members. Since age at first prospecting foray and age at emigration are positively correlated in male meerkats (Fig. 5.1), there was a similar positive trend between submissions involving the dominant female and relative age at emigration (Spearman rank correlation: r_s=0.435, N=19, P=0.061). In males, relative frequency of dominance competition was unrelated to relative age at first prospecting foray or emigration.

Among females, there was no relationship between relative age at first eviction or emigration and relative frequency of submissions (either total submissive interactions, or submissions to the dominant female; Spearman rank correlation: eviction/total: r_s= -0.305 N=17 P=0.23; eviction/dominant female: r_s= 0.049 N=17 P=0.496; emigration/total: r_s= 0.332 N=17 P=0.189; emigration/dominant female: r_s= 0.057 N=17 P=0.824). However, there was a negative correlation between relative age at first eviction and relative frequency of competition with littermates (Spearman rank correlation: r_s= -0.497 N=17 P=0.041).

During the course of the study, 27 study animals (13 males and 14 females) emigrated from their natal group in the company of an individual whose same-sexed littermate did not join the dispersing party (although most of these animals did disperse themselves). A comparison of the dominance interactions a study animal shared with its future dispersal partner, with those that it shared with the matched control with which it did not disperse, revealed that meerkats were involved in significantly fewer directional dominance interactions (as subadults in their natal group) with their future dispersal partner (Fig. 8.7). However, there was no difference in the number of competitive interactions that subadults shared with their future dispersal partner as compared with the control with which they did not disperse (Fig. 8.7).

Figure 8.7. Mean number of status-related agonistic interactions that subadult meerkats shared with their future dispersal partner, and the mean number shared with a same-sexed, same-aged control that did not join their dispersal party (Wilcoxon signed-rank: competitive interactions: W= -3.0, N=27, P=0.91; directional interactions: W=34.0, N=27, P=0.016). Vertical lines indicate SE.



8.5 DISCUSSION

Overt displays of aggression and submission were not a prominent feature of meerkat society; in fact, such interactions occurred at less than half the frequency reported for dwarf mongooses, *Helogale parvula*, living in the Serengeti (Creel et al. 1992). When directional dominance interactions did occur within meerkat groups, a member of the alpha pair was usually involved, and two-thirds of all submissions undertaken by subadult meerkats were elicited by the group's alpha female, confirming her strong social influence. Young females submitted to the alpha female ten times more often than did their male counterparts, and this is consistent with our knowledge of the dominant female's control over the breeding and emigration of subordinate females (Clutton-Brock et al.1998a; O'Riain et al. 2000). However, she also appears to play a hitherto unrecognized role in male emigration, with frequency of submission to the alpha female (but not to other group members) being positively correlated with length of tenancy in the natal group for males.

Although subordinate females are known to become increasingly submissive toward the alpha female immediately prior to their eviction from the group (T. H. Clutton-Brock unpublished), there was no relationship between rate of submission to the alpha female, prior to adulthood, and age at first eviction (both measured relative to same-sexed littermates). If submissive behaviour effectively mollified the group's dominant female, one might expect a positive relationship between these variables, although this would be negated if females that were least favoured by the dominant responded by submitting more frequently. Age at first eviction was, however, negatively correlated with frequency of competition with littermates, and this relationship was probably caused by body weight, since heavier females both competed more frequently and are more prone to eviction (Clutton-Brock et al. 1998a) than their smaller siblings.

Although displays of aggression and submission between non-dominant group members were rare, rank did appear to be age-dependent, with older group members enjoying social dominance over younger animals. The relationship between age and rank, however, was mutable, primarily because adults undergoing harassment by the dominant pair (females on the brink of eviction, immigrant males that had recently lost a fight for the dominant position, or animals returning to the group after a prolonged absence) behaved submissively towards all group members, and youngsters often capitalized on these temporary shifts in status. Thus subadults (which were rarely victimized by the alpha pair) almost never submitted to younger group members, yet directed one-third of their dominance assertions toward adults (Fig. 8.6). The finding that competitive dominance interactions were largely restricted to animals of the same age, and that when competition between animals of differing age did occur, it was almost always initiated by the older animal, is also consistent with the existence of an age-dependent hierarchy. Qualitative observations of banded mongooses, *Mungos mungo,* suggest that rank is also related to age in this species (Kingdon 1977), and age is known to account for 69% of the variance observed in dominance rank in dwarf mongooses (Creel et al. 1992).

This study also found some evidence that female meerkats were socially dominant to males. Although meerkats are sexually monomorphic in size (Clutton-Brock et al. 2002), subordinates of both sexes submitted much more frequently to the group's alpha female than to the alpha male. Similarly, although subadult males behaved equally submissively toward non-dominant elders of both sex, subadult females were only one-third as likely to submit to a male elder as to a female one. Females also initiated a greater proportion of intersexual competitive interactions than males, and this (based on the patterns of initiation seen between competitors of differing age or weight) suggests females enjoyed a competitive advantage over males. The social ascendancy of females in meerkat society is consistent with anecdotal observations made for other species of social mongoose: for example, in captive banded mongooses, females have been seen to dominate males (Rood 1986), and a study of dwarf mongooses living in the Serengeti found that the alpha female dominated the alpha male in seven out of eight groups (Creel et al. 1992).

While directional dominance interactions between non-dominant group members were rare, competitive interactions (in which both individuals simultaneously asserted dominance) were relatively common, with both subadults and natal adults indulging in competitive interactions eight times more frequently. Competition was most prevalent between same-sexed littermates (likely co-dispersers), and rate of competitive interactions, in females at least, was positively correlated with number of same-sexed littermates. Yet, despite these ongoing competitive interactions, dominance rank between same-aged animals was rarely resolved within the natal group, even in individuals of 2-3 years of age. Only when a vacancy arose for the dominant breeding position within a group (normally post dispersal), did same-sexed peers establish a clear dominance relationship through serious combat (Chapter 6).

The peak in competitive interactions observed in most litters at 11 months of age (averaging 1.51 interactions per hour; Fig. 8.3), and the ubiquitous fall in activity at 12 months of age (to 0.22 interactions per hour; well below the adult level of 0.65), appears to be associated with the onset of sexual activity, since most of the study's males also began undertaking prospecting forays (in pursuit of extra-group copulations; Young 2003) at 11 months of age (Chapter 5). Although frequency of agonism does vary seasonally in meerkats (with rates at their highest early in the breeding season, between June and September), the litters included in this study were born throughout the year (over an 18-month period) and thus seasonal factors, or short term fluctuations in environmental conditions, could not account for the widespread changes apparent at 11-12 months of age.

The high prevalence of competitive interactions observed among natal meerkats has not been recorded for other social mongooses (Creel et al. 1992), and is notable because it does not lead to the establishment of rank. Two factors are probably responsible for this unusual pattern of agonism. Firstly, meerkats living in their natal group do not actively compete with one another for any resource. Once foraging independently at 3 months of age, they do not compete for food (Barnard 2000), and their opportunities to breed are severely curtailed by inbreeding avoidance (O'Riain et al. 2000). As a consequence, the establishment of a fixed dominance hierarchy (whose purpose is to reduce the incidence of dangerous aggression arising from competition for scarce resources; Lack 1969; Marler 1976) is of little benefit to natal meerkats. This explains why directional dominance interactions among natal subordinates were both rare and of low intensity.

The second factor shaping meerkat competitive behaviour, is the species' marked reproductive skew. The high fitness benefits enjoyed by alpha animals (Clutton-Brock et al. 2001b) ensure that individuals will fight severely for the dominant position within a group. Since the costs of such battles are high (contestants frequently suffer grave injury), young natal meerkats cannot afford to seriously contest dominance rank with group members that may not even be present when access to a vacant dominancy eventually arises. Nevertheless, it is of considerable benefit to them to maintain a good knowledge of the competitive abilities of likely rivals (i.e. same-sexed littermates), and mutual competitive interactions allow them to evaluate both the strength and confidence of potential competitors. Although individuals did appear to be attempting to intimidate their rivals (e.g. those with a weight advantage competed more often and were more likely to initiate competitive interactions), individuals willingly dispersed with group members with which they had actively competed, even though they avoided animals with which they had shared directional dominance interactions (Fig. 8.7).

The prediction that meerkats of both sexes would show similar frequencies of agonistic behaviour was not fulfilled. Females indulged in status-related interactions much more frequently than males, and this was not simply due to appeasement behaviour toward the alpha female, as subadult females also interacted agonistically with other group members twice as often as their male littermates. In contrast to males, subordinate females' directional dominance interactions were primarily intrasexual, and the frequency of their competitive interactions (generally higher than males' - Fig. 8.3) was positively affected by number of same-sexed animals in their litter (Fig. 8.4). Considering that both male and female meerkats reap the same reproductive benefits from alpha status (parenting 75% of the pups raised by their group – Griffin et al. 2003), the finding that females invest more heavily in rank-related activities does not support the tenet that levels of agonism are proportional to the fitness benefits accruable from dominance. In this respect, meerkat behaviour also contrasts with that of dwarf mongooses (a species with a similar mating system), in which the sexes did not differ in rates of agonistic behaviour (Creel et al. 1992).

There are two possible explanations for the increased agonism seen in female meerkats. Firstly, the costs of failing to attain dominance may be higher for females than males. Dispersing females favour much smaller dispersal parties than males (Chapter 4), and are less likely to disperse with non-same-aged animals (older co-dispersers being more difficult to defeat) (Chapter 4) and this is consistent with an attempt to maximize their chances of winning dominance in their new group. While neither sex is likely to breed successfully as a subordinate (Clutton-Brock et al. 2001b), males can still obtain paternity by prospecting at neighbouring groups (Griffin et al. 2003), and they are more likely than females to challenge and supplant their group's established dominant (T. H. Clutton-Brock unpublished). Females that fail to win dominance in the group that they have helped found will ultimately be evicted by the alpha female, and - unlike males – they cannot join other established groups (Young 2003). The second potential factor contributing to high rates of agonism in female meerkats, is that, unlike males, females do occasionally attain the alpha position within their natal group (when the incumbent alpha female dies; Clutton-Brock et al. 1999b) and, although such events are rare (from a subordinate's perspective), this may contribute to a greater awareness of status among natal females.

CHAPTER NINE

DO MEERKATS USE PLAY TO CONTEST DOMINANCE RANK?

9.1 ABSTRACT

Of the many hypotheses that have been advanced to explain the adaptive significance of play, one asserts that social play functions to establish, maintain or contest social dominance rankings, thereby circumventing the need for harmful aggression. This study tested the hypothesis using data from a wild population of meerkats, *Suricata suricatta*, living in the Kalahari Desert. Contrary to the predictions generated by the hypothesis, play and agonistic behaviour were negatively correlated across development, frequency of play was not positively related to number of potential competitors in the group (in fact, play appeared to be inhibited by the presence of same-sexed littermates), and there was no sex difference in play even though females invested more heavily in agonistic behaviour. There was, however, a positive relationship between frequency of play and frequency of agonistic behaviour in individual females, and meerkats showed some preference for playing with their rivals. Nevertheless, the outcome of play fights did not influence a pair's agonistic behaviour, and winning during play was unrelated to how frequently an individual undertook, or initiated, competitive interactions. Similarly, dyads with a heavily biased play relationship (i.e. one individual usually won) were just as likely to indulge in competitive dominance interactions as dyads that were evenly matched in play. Play behaviour, however, did appear to be inhibited (both in frequency and behavioural content) by agonism, and an individual's behaviour during play seemed to reflect its social standing within the group. The study concluded that the primary purpose of play in young meerkats was not related to dominance rank.

9.2 INTRODUCTION

Many hypotheses have been advanced to explain the adaptive function of play (Smith 1982; Martin & Caro 1985) and one of these asserts that social play is used to establish or maintain social dominance rankings, thereby circumventing the need for dangerous aggression among group members or littermates (Carpenter 1934). Despite the popularity of this hypothesis (Dolhinow 1971; Poirier & Smith 1974; Geist 1978; Berman 1982; Paquette 1994), there is little available evidence to either support or refute it. Paquette (1994) found some indication that adolescent chimpanzees, *Pan troglodytes*, used play to challenge dominance relationships, but his study was restricted to four captive individuals whose play fights routinely escalated into real aggression. In contrast, Symons (1978a) found that rank-reversals in free-ranging rhesus monkeys, *Macaca mulatta,* did not derive from play, in fact, only individuals that were not actively competing for status engaged in play. He argued convincingly that play fights could not be used to establish rank and still remain playful because individuals would have to react to play invitations as they would to a threat or challenge (i.e. with either submission or escalation). Similarly, primate species in which dominance rank is fixed by maternal status, play no less frequently than species in which rank is mutable by physical contest (Smith 1982), and wild primates that are prevented from playing (by a scarcity of food) appear to enjoy normal dominance relationships (Baldwin & Baldwin 1974; Lee 1983).

This study assesses the relationship between social play and dominance-related behaviour in a non-primate, the meerkat, *Suricata suricatta.* Meerkats are social, cooperatively breeding mongooses that live in groups (of 3-40 individuals) normally comprised of a dominant breeding pair, the pair's offspring, and a few immigrant males (Clutton-Brock et al. 2001b). Although young meerkats attain sexual maturity at 7-11 months of age, they delay dispersal from their natal group until approximately 2 years of age (Chapter 5). Social rank among natal group members appears to be age-dependent, although overt displays of aggression and submission between natal animals are rare, and competitive interactions (in which both animals attempt, simultaneously, to assert their dominance) occur eight times more frequently (Chapter 8). Competitive interactions are primarily directed at same-sexed littermates, but dominance rank is rarely resolved between same-aged animals within the natal group (Chapter 8). Female meerkats are involved in three times as many agonistic interactions as males, and they also appear to be socially dominant to males (Chapter 8).

Female meerkats are forcibly evicted from their natal group by the dominant female (when she is in the latter stages of pregnancy), and frequently suffer several short-term evictions before eventually dispersing (Clutton-Brock et al. 1998a). Male meerkats appear to leave their natal group voluntarily after undertaking a series of short-term prospecting forays to neighbouring groups from around 11 months of age (Young 2003). Meerkats of both sexes normally disperse in the company of one or more same-sexed group members, most commonly littermates (Chapter 4), and they either found new groups with opposite-sexed dispersers from other groups or, in the case of males, join or take-over established groups (Doolan & MacDonald 1996b; Young 2003). Co-dispersers then fight one another ferociously to obtain the reproductively lucrative dominant position within the group (Chapter 6). Once established, the group's dominant breeding pair monopolizes around 75% of the group's reproductive effort (Clutton-Brock et al. 2001b), and enjoys social dominance over all other group members (Chapter 8).

If the primary purpose of social play in meerkats is to establish, maintain or contest dominance rank, we would expect the following: (1) a concurrence between rates of dominance-related behaviour and social play across development; (2) a positive relationship between frequency of competitive dominance interactions and social play in individuals; (3) a positive relationship between the number of potential competitors in a group and frequency of play; (4) a preference during play for primary competitors; (5) a concurrence in sex differences between agonistic behaviour and social play; (6) a negative relationship between losing play fights and initiating competitive dominance interactions; and (7) a positive relationship between success in play fights and social status. This study tests these predictions by examining the behaviour of young meerkats (less than 12 months of age) living in their natal group, in a wild population in the Kalahari Desert.

9.3 METHODS

I carried out the study between August 1999 and September 2003, working on a natural population of meerkats living on ranchland in the southern Kalahari Desert, 30 km west of Van Zylsrus, South Africa (26°58'S, 21°49'E). See Section 1.6 for details of the study site's topography, vegetation and rainfall. The work was carried out under licenses issued by the Northern Cape Conservation Service, South Africa. All meerkats in the study were habituated to close observation and handling, and were individually marked with permanent marker pen on the tail, plus a small patch of snipped fur on the body, which were both applied unobtrusively while the animals were sunning at the burrow. All study animals were monitored several times a week, from birth until they died, dispersed from their natal group or attained at least 36 months of age. All dispersing individuals were observed after they had left their natal group and most were followed until they established or joined another group.

I collected data on social play (also referred to as play fighting), allogrooming and dominance-related behaviour for eight litters of meerkats (42 individuals) from six groups, throughout their first 12 months of life. Additional data was collected for one litter (seven individuals) during the juvenile and subadult periods only. Two of the study litters were comprised of pups borne by more than one female, but the youngsters (within 2 weeks in age) were raised together as a single litter, and were treated as such in the analysis.

I documented dominance-related agonistic interactions ad libitum (Altmann 1974), whenever an interaction involving a study animal was observed (competition over food was excluded), resulting in a sample of 917 interactions (mean 102 per study litter). A detailed description of agonistic behaviour in meerkats (and the definitions used in this study) can be found in Section 8.3. I classified an interaction as 'submissive' if the study animal exhibited submissive behaviour (see Chapter 8) toward another group member, regardless of which animal initiated the interaction. I classed an interaction as 'competitive' if both participants attempted to assert their dominance (see Chapter 8), and these interactions normally consisted of mutual, synchronous hip-slamming or head shaking (Chapter 8).

A detailed description of how I documented play behaviour (including the frequency of social play) can be found in Chapter 6, and Section 1.5.4 describes the behavioural components of meerkat social play. In this study, I recorded the following elements: wrestling (one animal lies on its back while the other stands on or over it, pinning it the ground; Fig. 4.1a), mounting (Fig. 4.1b), chasing and grappling (animals stand bipedally, clasping each other with their forelegs and attempting to push one another over; Fig. 4.1c). When assessing play fighting success, I analyzed all play bouts that included play wrestling, and classified the dominant 'on-top' wrestling position as the winning position, and the submissive 'on-the-bottom' position as the losing position (Thompson 1998). Role reversals did sometimes occur within a single play bout, in which case both players were credited with both winning and losing the wrestling bout, and hence percentages do not necessarily add to 100. A detailed description of how I calculated disparity in play fighting success, in littermate dyads, can be found in Section 7.3.4. To compare litters that contained a single female with those that contained multiple females, I collected additional play data for five extra litters of meerkats (23 individuals) at 5-7 months of age. Unfortunately, time constraints prevented me from addressing this question for both the sexes, and I selected females because they are involved in more agonistic interactions and, unlike males, the frequency of their competitive interactions is positively related to number of same-sexed littermates (Chapter 8).

A detailed description of how allogrooming data was collected and defined can be found in Section 4.3.6. In all analyses, age classes were defined as follows: pup, less than 3 months old; juvenile, 3-6 months old; subadult, 6-12 months old; and adult, over 12 months old. I used parametric statistical tests throughout the analyses except where the data differed significantly from a normal distribution (based on the Kolmogorov-Smirnov test for normality). In these cases, I used equivalent nonparametric tests. All statistical tests were two-tailed with a significance threshold of 0.05. Means are given +/- SE.

9.4 RESULTS

9.4.1 Frequency of play and status-related interactions

During the course of development, frequency of play (measured as the percentage of one/zero scans at the burrow in which a meerkat played) was negatively correlated with frequency of both competitive and submissive status-related interactions (Pearson correlation: submissions: r_9= -0.714, P=0.014; competition: r_9= -0.686, P=0.020; Fig. 9.1).

The relative frequency of play shown by individual subadults was positively correlated with relative frequency of competitive interactions for females (Spearman rank correlation r_s=0.546, N=13 P=0.052), particularly competition with littermates (Pearson correlation: r_{11}=0.63, P=0.021), but was not related in males (r_{19}=0.358, P=0.111). Frequency of play was also positively related to relative frequency of submissive interactions (Pearson correlation: r_{30}=0.391, P=0.027).

Mean rate of play, in study litters, was not related to either group size or litter size, at any age (Chapter 5), and nor was it correlated with number of same-sexed, non-dominant animals in the group, for subadults of either sex (females: Pearson correlation: r_5=0.106, P=0.821; males: Spearman rank correlation: r_s=0.536, N=7, P=0.181). The number of same-sexed littermates was negatively correlated with mean rate of play in subadult males but was unrelated to play in subadult females (Fig. 9.2). However, females (aged 5-7 months) with no same-sexed littermates played significantly more frequently (relative to their litter's mean) than females with multiple same-sexed littermates (Fig. 9.3).

Figure 9.1. Mean frequency of play fighting, submissive interactions and competitive interactions (defined in Section 8.3) by age, in (a) males (Pearson correlation: play/subm.: r_9= -0.751, P=0.008; play/comp.: r_9= -0.626, P=0.039) and (b) females (play/subm.: r_9= -0.688, P=0.019; play/comp.: r_9= -0.675, P=0.023.)

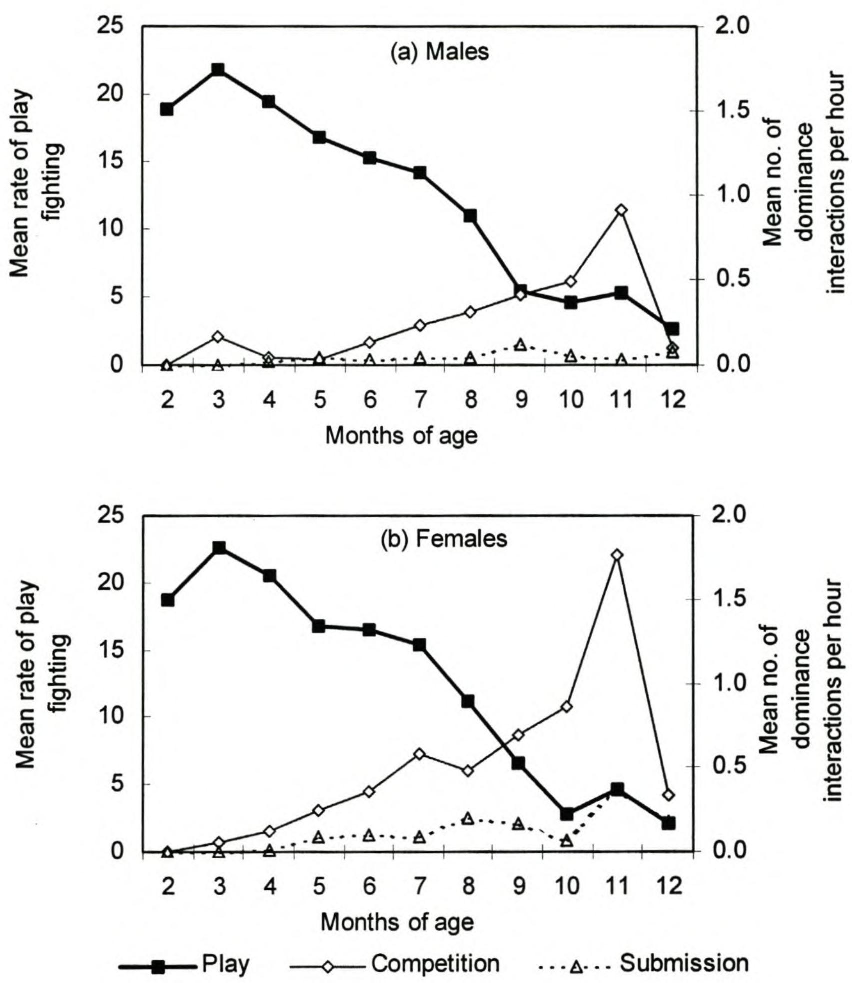
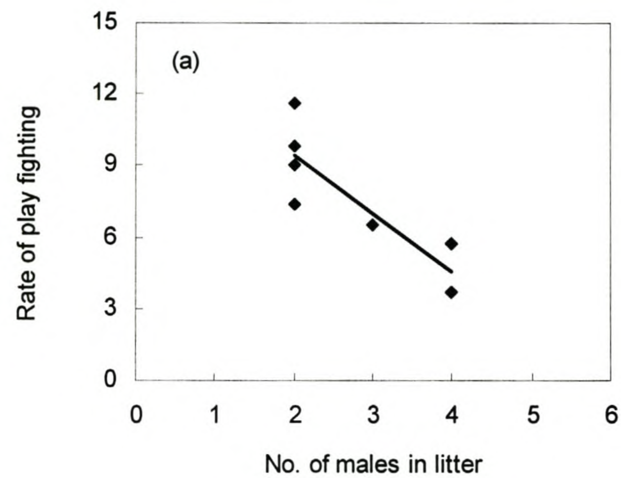
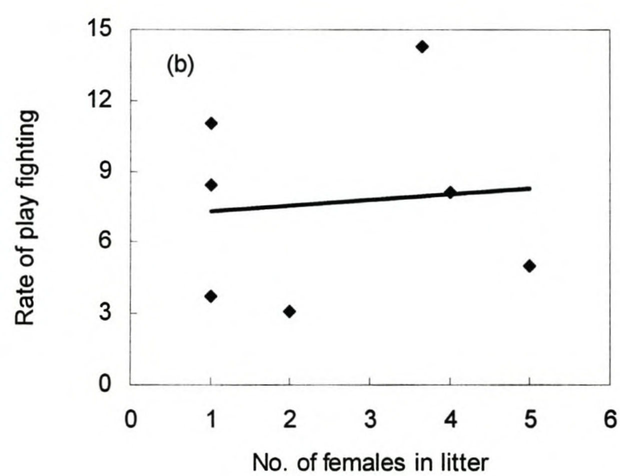


Figure 9.2. Mean rate of play in subadults as a function of number of same-sexed animals in the litter, in (a) males (Spearman rank correlation: r_s= -0.896, N=7, P<0.001) and (b) females (Pearson correlation: r_5=0.142, P=0.762).



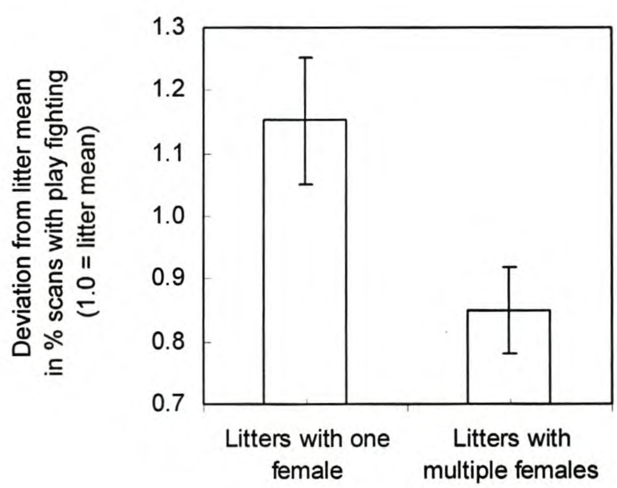


9.4.2 Partners during play and competitive dominance interactions

Young meerkats strongly favoured same-aged partners (i.e. littermates) during both competitive dominance interactions (Fig. 8.6) and social play (Fig. 4.1). However, while meerkats primarily directed competitive interactions toward littermates of their own sex (Chapter 8), they showed no preference for same-sexed littermates when playing (Chapter 4); in fact females appeared to avoid playing with same-sexed littermates once the attained sexual maturity (at 9-12 months of age; Chapter 4).

Among same-sexed littermates, pairs of subadults that competed with one another more frequently than the average for their litter, also played together more frequently (Fig. 9.4). Since play partner preferences among same-sexed littermates (measured as the relative number of play bouts a dyad shared) remained consistent between the juvenile and subadult periods (Spearman rank correlation: r_s=0.383, N=41, P=0.014), the frequency of play shown by juvenile dyads was also positively correlated with frequency of dominance competition as subadults (r_s=0.399, N=41, P=0.01). There was, however, no relationship between how frequently a dyad played (or competed) and how frequently it allogroomed (Fig. 9.4; competition/allogrooming: r_s= -0.168, N=35, P=0.333).

Figure 9.3. Mean rate of play (relative to litter mean) in females (aged 5-7 months) from litters with multiple female members (mean 3.6; N=7) and those with only one female member (N=6). All litters included at least two male members (mean 2.4). Vertical lines indicate SE. (t test: t_{11}=2.217, P=0.049.)



9.4.3 Sex differences in play behaviour

Meerkats exhibited very few sex differences during play, with both sexes exhibiting a similar developmental profile for play (Chapter 6), and playing at the same frequency throughout their first twelve months of life (Fig. 6.2). The behavioural composition of social play (i.e. the frequency of wrestling, grappling, chasing or mounting) also did not differ between the sexes in pups and subadults, but juvenile males did wrestle slightly more frequently (wrestling during 41.9% of their play bouts compared with 38.9% in females;

paired t test: t_8=3.027, P=0.016) and females undertook grappling slightly more often (14.5% of bouts compared with 12.3% in males; t_8=2.597, P=0.032). However, as meerkats aged, females won an increasingly higher proportion of their play wrestling bouts than males (Chapter 6); in fact when opposite-sexed subadult littermates play wrestled, the female partner won almost two-thirds of the time (Fig. 9.5).

Figure 9.4. The frequency with which same-sexed littermate dyads played as a function of the frequency with which they undertook (a) competitive dominance interactions or (b) allogrooming (all measured relative to the litter's mean dyad). (Competition: Pearson correlation: r_{39}=0.438, P=0.004; allogrooming: Spearman rank correlation: r_s=-0.119, N=35, P=0.493).

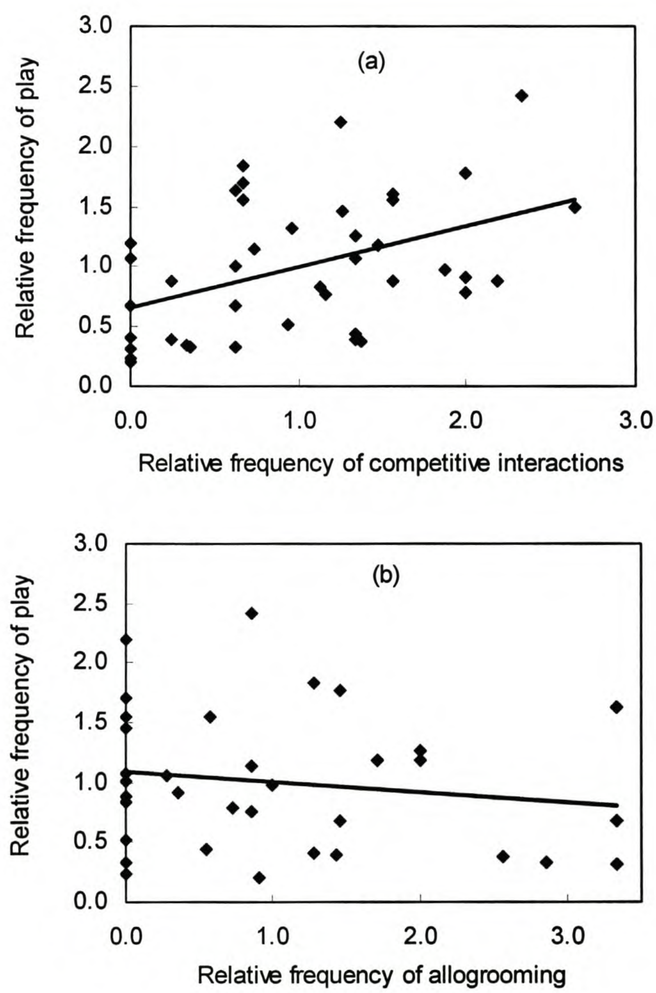
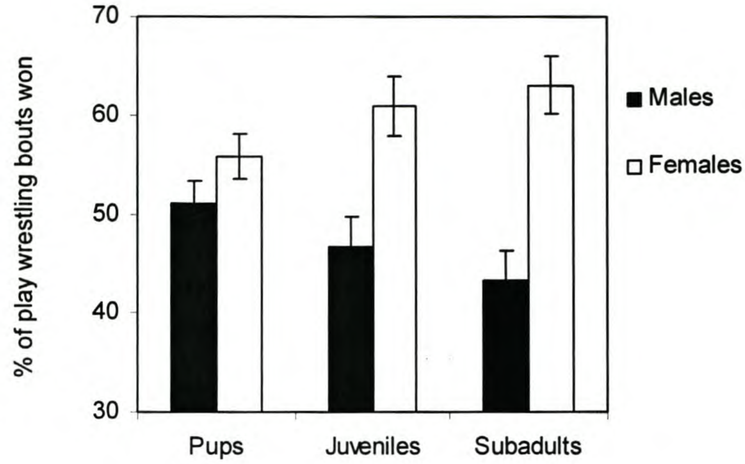


Figure 9.5. Play wrestling in mixed-sexed littermate dyads: percentage of bouts won by males versus females. (Sex difference: t test: pups: t_{108}=1.484, P=0.141; juveniles: t_{124}=3.384, P<0.001; subadults: t_{116}=4.733, P<0.001.) Vertical lines indicate SE.



Although meerkats exhibited few sex differences in play, subadults behaved differently when playing with same-sexed partners than when playing with partners of the opposite-sex. Same-sexed littermate dyads were less likely to undertake 'directional' elements of play fighting (i.e. behaviours in which win/lose roles were pronounced; Biben 1998) such as chase/flee behaviour (t test: t_{113}=3.374, P=0.001) and wrestling (Fig. 9.6). This was not the case in meerkats under 6 months of age, which did not appear to discriminate between partners on the basis of sex (Fig. 9.6). Hip-slamming (a prominent component of competitive dominance interactions; Chapter 8) was rarely included in meerkat play fighting, but its prevalence increased significantly in subadult animals (rising from 0.6% of bouts in juveniles to 1.6% in subadults; paired t test: t_8= -2.884, P=0.020). Dyads of same-sexed subadults were almost six times as likely to include hip-slams in their play bouts as mixed-sexed subadult dyads (Fig. 9.7).

Figure 9.6. Relative percentage of play bouts that included wrestling, during play by mixed-sexed and same-sexed littermate dyads (t test: pups: t_{102}=1.163, P=0.247; juveniles: t_{120}=1.651, P=0.101; subadults: t_{113}=3.057, P=0.003). Vertical lines indicate SE.

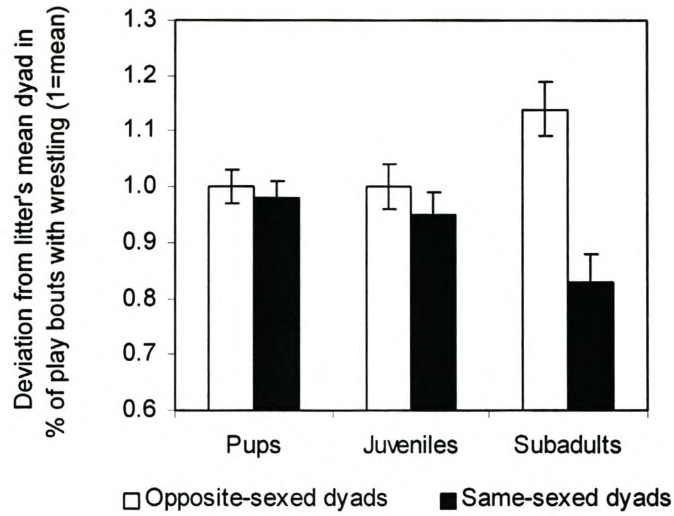
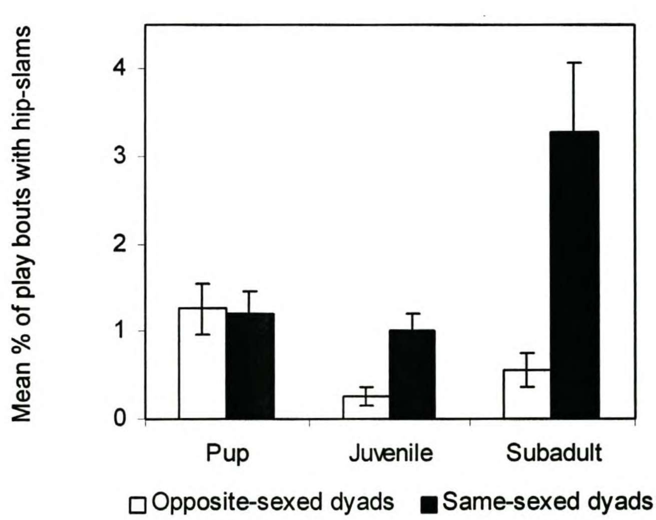


Figure 9.7. Mean percentage of play bouts that included hip-slams, by age, in dyads of same-sexed or opposite-sexed littermates (paired t test: pups: t_7=0.283, P=0.785; juveniles: t_8= -3.120, P=0.014; subadults: t_8= -4.026, P=0.004). Vertical lines indicate SE.



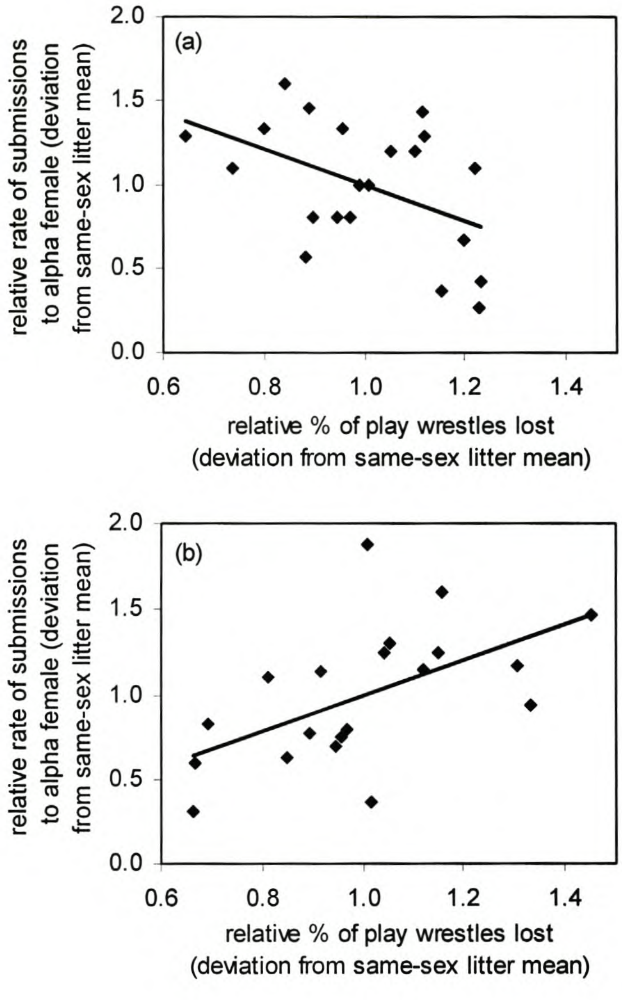
9.4.4 Play fighting success

The relative tendency to lose play fights (i.e. adopt the subordinate position when play wrestling) was strongly positively correlated with relative frequency of submissions in females (Pearson correlation: r_{18}=0.701, P=0.001). Males showed the reverse trend, with relative likelihood of losing play fights negatively correlated with relative frequency of submitting to the group's dominant female (Fig. 9.8). There was no relationship between tendency to lose play fights and frequency of dominance competition, for either sex (males: Pearson correlation: r_{19}= -0.064, P=0.782; females: Spearman rank correlation: r_s=0.112, N=20 P=0.635).

In dyads of same-sexed littermates, the outcome of play fights had no apparent affect on competitive dominance interactions. The level of disparity in winning that a dyad exhibited during play (either as juveniles or as subadults) was not correlated with the frequency with which the pair undertook competitive interactions as subadults (Pearson correlation: juvenile play: r_{38}= -0.069, P=0.673; subadult play: r_{38}= -0.071, P=0.663). Nor was there any correlation between the likelihood of winning play fights with a same-sexed littermate and the likelihood of being the initiator of competitive interactions with that littermate (r_{31}= -0.014, P=0.937).

Play fighting success, however, was correlated with length of tenancy in the natal group. Subadult males that lost play wrestling bouts more frequently than their male littermates tended to begin prospecting at a younger age (Pearson correlation: r_{19}= -0.439, P=0.047) and to emigrate from their natal group earlier than their brothers (Spearman rank correlation: r_s= -0.572, N=21, P=0.007). Females showed the opposite trend, with subadults that lost most frequently emigrating later than their same-aged sisters (Spearman rank correlation: r_s= 0.535, N=11, P=0.082), but there was no relationship between play fighting success and age at first eviction (Pearson correlation: r_{19}=0.139, P=0.683).

Figure 9.8. Frequency of adopting the subordinate position in play wrestling bouts (relative to same-sexed littermates) as a function of frequency of submissive interactions directed toward the group's dominant female (relative to same-sexed littermates), in (a) males and (b) females. (Pearson correlation: males: r_{19}= -0.462, P=0.035; females: r_{18}=0.559, P=0.010).



9.5 DISCUSSION

The behaviour of young meerkats only partially met the predictions generated by the hypothesis that social play is used to contest or assert dominance rank. As observed in other taxa (Smith 1982; Drea et al. 1996), social play and dominance-related behaviour in young meerkats were negatively correlated across development (Fig. 9.1). This was the reverse of the relationship predicted by the hypothesis, and is consistent with earlier findings that aggression inhibits play in this species (Chapter 3). Once agonistic interactions escalated, young meerkats not only played less frequently, they also shared fewer play bouts with littermates (their main competitors); e.g. 87% of play bouts in pups were shared with littermates, compared with only 47% in animals 9-12 months old (Chapter 4).

The second prediction (that frequency of play will be positively related to frequency of competitive interactions among individuals) was met by female meerkats but not by males (although it is possible that a weaker relationship existed in males but did not attain statistical significance due to small sample size). Although this relationship between play and competition appears to support the tenet that meerkats are playing and competing for the same reason (i.e. to contest status), such an interpretation cannot explain why play was also positively related to frequency of submissive behaviour, since lower ranking animals (that submit more frequently) should want to avoid 'playful' demonstrations of status. Similarly, unlike frequency of competitive dominance interactions (Fig. 8.4), frequency of play was not positively related to the number of potential competitors in the group (as would be expected if individuals had to test, or try to intimidate, each of their rivals – prediction number three). In fact, frequency of play was negatively correlated with number of same-sexed littermates in males (Fig. 9.2), and females with no same-sexed animals in their litter actually played more frequently (relative to the average for their litter) than females with same-sexed littermates (Fig. 9.3).

As predicted by the hypothesis (prediction number four), same-sexed littermates that competed with one another most frequently also played together most frequently. This relationship was unlikely to be a product of proximity because it did not extend to allogrooming (Fig. 9.4), which, like the other two behaviours, occurs most commonly when group members are socializing together at a burrow. However, in contrast to this finding, young meerkats devoted just as much time to playing with opposite-sexed peers (with which they rarely competed; Chapter 8) as same-sexed peers (their most important rivals; Chapter 8) suggesting that the primary purpose of play was not status-related. Similarly, female meerkats played no more frequently than males (Fig. 6.2), even though they were involved in three times as many agonistic interactions (Chapter 8).

The most telling evidence against the hypothesis arises from an examination of the outcome of play fights. If meerkats were using play to contest dominance, or to assess the competitive abilities of potential rivals, we would expect the degree of success they showed during play fights to be related to their behaviour during competitive dominance interactions.

We know, for example, that animals with a size advantage over their littermates are more likely to initiate dominance competition with their peers (Chapter 8), so it is reasonable to expect habitual winners of play fights to be more eager to indulge in competition than habitual losers. However, this was not the case, with no relationship between play fight success and frequency of dominance competition. Dyads of same-sexed littermates that shared a heavily biased play relationship (i.e. one individual nearly always won their shared play fights) were just as likely to indulge in competitive dominance interactions as dyads that were evenly matched in play, and the winning individual was no more likely than the loser, to be the initiator of such interactions. Clearly, defeat during play did not deter an individual from contesting status with the victor, and perhaps this is understandable given that success in play fighting is not predictive of future success in serious fights for a vacant dominancy (Chapter 6).

Although young meerkats did not appear to modify their behaviour toward one another in response to their play experiences, social play was not unaffected by the increasing agonism associated with the approach of sexual maturity. The physical parameters that shaped play behaviour in pups and juveniles - e.g. the effects of nutritional state on frequency of play (Chapter 2), and the effect of disparity in body weight on play partner preference and wrestling success (Chapter 7) – did not influence play in subadults (Chapter 5; Chapter 7). Instead, frequency of play in this age group was negatively related to the presence of same-sexed peers (Fig. 9.2; Fig. 9.3) and littermates of the same sex played together less frequently than expected in 9-12 month-olds (Chapter 4). Unlike younger animals, subadults avoided initiating play with peers that defeated them more than 80% of the time (Fig. 7.7) and with same-sexed (but not opposite-sexed) littermates that had frequently defeated them when they were juveniles (Chapter 7). Play bouts between same-sexed subadults also differed in composition from bouts between partners of mixed sex, not only because of the incorporation of elements of competitive behaviour (Fig. 9.7), but by the reduction in behaviours that accentuated win/lose roles (Fig. 9.6). A similar reduction in the prevalence of directional components of play fighting occurs in the play of meerkat pups subject to frequent aggression by their littermates during foraging (Chapter 3), confirming that it was the escalation of agonistic interactions that shaped and constrained play in subadults.

The final prediction generated by the hypothesis, that play fighting success will be positively correlated with social status, appeared to be met by female meerkats. Female subadults that habitually lost play fights displayed submissive behaviour more frequently (Fig. 9.8), and tended to disperse from their natal group later, than littermates that routinely won. Yet the increased submissions exhibited by losers of play fights were directed toward older same-sexed group members, with which young females rarely played (Chapter 4), and those individuals to which females were losing play fights (mostly littermates) did not discriminate between losers and winners during competitive dominance interactions. Similarly, relative age at first eviction from the group was unrelated to play fighting success, suggesting that the dominant female (which controls eviction) did not differentiate between subordinates on the basis of play success (or the factors that determined such success). It therefore appears likely that group members were not using play to learn about an individual's abilities or social standing but, rather, an individual's behaviour during play reflected its status within the group. It is conceivable that losses during play sapped a young female's confidence (Sutton-Smith & Kelly-Byrne 1984; Biben 1998) resulting in increased submissive behaviour towards the group's more intimidating members, and hesitancy to leave the security of the natal group. However, if such self-assessment was occurring during social play, we would expect habitual losers of play fights to avoid initiating competitive interactions with the individuals that beat them, and this was not the case.

The relationship between play fighting success and concurrent dominance rank has been assessed in a number of species, and although no correlation was detected in domestic horses, *Equus callabus* (Araba & Cromwell-Davis 1994), red-necked wallabies, *Macropus rufogiseus* (Watson 1993), rhesus monkeys (Symons 1978a) or female baboons, *Papio anubis* (Owens 1975), a positive relationship was found in squirrel monkeys, *Saimiri sciureus* (Biben 1998) and male baboons (Owens 1975). Biben (1998) asserted that this positive relationship was a result of squirrel monkeys 'playing to win' so play fighting provided an accurate measure of competitive ability and was positively related to status. This is probably also true, to some degree, of young meerkats, since play fighting success is positively related to success during fights over food in meerkat pups (Fig. 7.1). However, an alternative explanation is that low ranking individuals may be reluctant to confront higher-ranking animals, even in play, and thus they avoid adopting the dominant role during play fights. The finding that female meerkats win an increasing proportion of their play bouts as they approach adulthood (Fig. 9.5) suggests that this is also a factor influencing meerkat play. Since meerkats are sexually monomorphic (Clutton-Brock et al. 2002) and the sexes do not differ in play behaviour, the increasing success of females is almost certainly a result of the males' growing deference to the social dominance of females (Chapter 8), as their awareness of social status develops.

In direct contrast to females, male meerkats that habitually lost play fights submitted less frequently to the group's dominant female (Fig. 9.8) and left their natal group earlier than their brothers (both to prospect and to disperse). Since emigration and frequency of submission are positively correlated in male meerkats (Chapter 8), it is difficult to ascertain the role of play success, and our ignorance of the factors promoting male dispersal prevents us from knowing whether the behaviour of losing males was indicative of low status. However, males that frequently lost play fights did not submit more often to same-sexed group members (potential rivals), as would be expected if meerkats were using play to establish rank.

In conclusion, it appears that the primary function of social play in meerkats is not the establishment, maintenance or contesting of dominance rank. The competitive testing of same-sexed peers - in the form of highly ritualized, mutually aggressive interactions (hip-slamming, head-shaking and rearing; see Section 8.3) - is a prominent feature of the social life of young meerkats (Chapter 8), and stands testimony to the importance of meerkats knowing the relative size, strength and disposition of individuals that, one day, may compete with them for a vacant dominancy. Although play fighting could potentially provide meerkats with much more detailed information about the fighting skills and competitive abilities of rivals, there is no evidence that meerkats are using feedback from play in this way. Nevertheless, play was not divorced from the social milieu of the group, and meerkats over 6 months of age modified their play behaviour to avoid confrontation. As a consequence, the behaviour an individual showed during social play tended to reflect its social standing within the group.

CHAPTER TEN

GENERAL DISCUSSION

10.1 OVERVIEW

Play is a highly conspicuous behaviour that has attracted the attention of scientists for more than a century (e.g. Groos 1898; Spencer 1898). The apparent purposeless of play (a defining characteristic), and hence its seeming violation of the tenets of natural selection, has engendered much speculation (Muller-Schwarze 1971), with researchers postulating at least 30 potential explanations of the adaptive benefits of play (see Section 1.3). Unfortunately, most of these hypotheses remain little more than 'Just-So-Stories' due to a lack of data to either support or refute them, and their popularity appears to wax and wane according to fashion rather than the accumulation of quantitative evidence (e.g. the widespread acceptance of the practice hypothesis – Smith 1982, Caro 1988 – has diminished in recent years – Bekoff & Byers 1998 – despite the acquisition of little new evidence). Most importantly, rigorous hypothesis-testing studies of play are exceptionally rare.

This regrettable 'state of play' has arisen because play is inherently difficult to study. For a number of years, play research was hampered by semantic disputes over how play should be defined (Lorenz 1956; Hinde 1970; Bekoff & Byers 1981; Fagen 1981; Martin 1984a), and a reluctance to accept play as a valid behavioural category (Welker 1971; Lazar & Beckhorn 1974). While these issues are no longer debated, the challenges created by play's unique characteristics are not so readily resolved. Play is a relatively rare behaviour (occupying only around 3-5% of a young mammal's time; Bekoff & Byers 1992), and it tends to occur sporadically and unpredictably, and – in many species – is restricted to a short developmental window. This makes data collection difficult and time-consuming, and it is often impossible to obtain accurate data on play (which is active and fast-moving) for wild animals in situ. As a consequence, field studies of play are a rarity and largely limited to a handful of species of ungulate, pinnaped and primate. Most play research has focused on captive animals, even though captivity distorts many of the parameters known to influence play - such as food accessibility (Baldwin & Baldwin

1976; Muller-Schwarze 1982) and group composition (Biben 1998) - and precludes any evaluation of play's downstream effects on important life history variables. More problematic, however, is the fact that it is virtually impossible to manipulate a young animal's play experience (e.g. reduce the amount of time it devotes to play) without generating a plethora of confounding variables (Bekoff 1976) and contravening animal-research ethics.

Although subject to these constraints, this study set out to quantitatively assess a number of hypotheses relating to play's function, using data collected from a natural population of small, social carnivore. Only those hypotheses that predicted benefits which were of great potential importance to the inclusive fitness of the study species were evaluated, and a variety of non-invasive means (e.g. capitalizing on natural variation in individual play behaviour) were used to obtain evidence that would either support or refute the hypotheses. The study found that although play in young meerkats does carry an energetic cost, with youngsters modifying their frequency of play in response to their energy intake (Chapter 2), none of the hypotheses of function evaluated by this study was able to account for the persistence of play behaviour in this species, or to identify the adaptive benefits that meerkats derived from play. Play did not increase 'social harmony' by reducing aggression between playmates (Chapter 3), and nor did it strengthen an individual's bonds to its social group, such that it remained in the group for longer, or contributed more to the group's cooperative activities (Chapter 4). There was no evidence that meerkats used play to strengthen alliances, and youngsters played no more frequently with their future dispersal partners than with controls with which they did not disperse (Chapter 5). Play fighting experience did not appear to improve a meerkat's fighting skills, and individuals that ultimately won dominance of a group (through fighting) had played no more frequently, and no more successfully, than the littermates which they defeated (Chapter 6). Although play behaviour in meerkats was affected by intragroup aggression (Chapter 2 & Chapter 9), meerkats did not use play to contest, assert or establish dominance status (Chapter 9), and there was little evidence to suggest that their preference for well-matched play partners arose from their use of play for self-assessment (Chapter 7). Although the unremitting negativity of these results may appear daunting, these findings are of considerable importance because they are able to tell us a great deal more about play behaviour than would a positive result.

Play is believed to have evolved in the earliest of mammals (Byers 1984) and while it persists in all mammalian orders (Fagen 1981), we do not know whether extant species play for the same reasons as their ancestors. After 70 million years of natural selection, it is certainly possible that different taxa garner quite different fitness benefits from their play. Meerkats, as members of the mongoose family, belong to an order that is predominantly solitary (Carnivora), and the earliest-known ancestral mongooses almost certainly pursued a solitary lifestyle (Veron et al. 2003), as do three-quarters of the 37 extant species of mongoose (Estes 1991). Yet despite this phylogenetic propensity for a solitary way of life, the social mongooses (believed to be a monophyletic group - Veron et al. 2003) have evolved some of the most complex social systems known in mammals. The strong selection pressures that led these mongooses to set aside their inherited antipathy for conspecifics and develop complex, cooperative societies, would certainly have favoured any mechanism which reduced intragroup aggression and promoted cooperation; and there appears to be little reason why social play should not provide such a mechanism. Because play is pleasurable (Humphreys & Einon 1981; Normansell & Panskepp 1990; Calcagnetti & Schechter 1992; Pellis & McKenna 1995), it provides players with positive reinforcement, so during social play participants enjoy strong positive social conditioning, which could easily strengthen social bonds (Baldwin 1982). If this were the case, we would expect the social-bonding properties of play to have been strongly favoured during the evolution of mongoose sociality, and thus be apparent in meerkat play behaviour today. This study shows that they are not (Chapters 3, 4 & 5). While a positive result would have told us only that meerkats (and probably all social mongooses) use play to strengthen social ties, this study's negative finding - that meerkats, despite every reason to do so, do not use play in this way - provides us with strong evidence that social play does not have the capacity to strengthen social bonds. Therefore we can predict that other species of mammal are unlikely to play for this purpose. Similarly, the findings that meerkats - which show high levels of reproductive skew (Clutton-Brock et al. 2001c) and thus reap huge reproductive rewards from winning dominance of a group - do not use play to either improve their fighting skills (Chapter 6) or to establish dominance over their competitors (Chapter 9), suggest that play is unlikely to be able to provide such fitness benefits to any species.

10.2 LIMITATIONS OF THE STUDY

Before accepting the findings of this study, it is essential to assess the limitations impacting upon the work, and evaluate any factors that may jeopardize the validity of the results. One such factor is the issue of sample size: i.e. was the study's sample large enough to allow the null hypothesis (in this case, that play and various outcome variables were not related) to be rejected, if biologically meaningful relationships had actually existed. The difficulty of attaining adequate sample sizes is very familiar to researchers of mammal behaviour, and the problem is exacerbated if long-term longitudinal data is required, particularly in wild populations where losses are inevitable. Nevertheless, I made every effort to maximize the number of individuals and litters sampled (within the time constraints imposed by doctoral research), obtaining baseline longitudinal data from eight main focal litters, plus supplementary material from additional litters to raise the sample sizes for questions of particular importance. As a consequence, the majority of statistical tests used in the study had sufficient power to confidently reject the null hypotheses (80% of the time if a medium-sized effect had occurred), according to post-hoc power analyses (Thomas & Juanes 1996). Although a few of the analyses were found to be statistically weak, their findings were consistently corroborated by other, more robust, tests. However, since the validity of such post-hoc power analyses is controversial (Hoenig & Heisey 2001), it may be more valuable to note that the data almost never showed any trends that suggested the null hypotheses might be rejected if sample sizes were larger, and it seems extremely unlikely that the negative findings of this study were the result of erroneous acceptance of the null hypotheses because of small sample sizes.

Another factor that could potentially impact on the validity of the study's findings is the degree to which frequency of play varied between individuals within the study population. Because of the difficulties inherent in experimentally manipulating an animal's rate of play (Martin & Caro 1985; Bekoff 1976), particularly in a wild population, this study capitalized primarily on naturally occurring variation in play behaviour, and comparisons between littermates formed the backbone of the study, because these individuals shared the same social and physical environments, eliminating an array of potential confounding variables (such as group size, group composition, prey abundance, season, etc.). However, it is conceivable that the play behaviour of littermates did not vary sufficiently to produce any discernable differences in the outcome variables that the study used to assess hypotheses of function. However, this seems unlikely because the degree of variation in the play behaviour of littermates was marked (and increased as animals aged), and it was significantly correlated with a range of variables (e.g. weight gain, age at emigration, frequency of submissive behaviour, etc.) suggesting that intralitter differences were large enough to make such analyses valid. Similarly, the results obtained from intralitter comparisons were generally corroborated by the results of other analyses, such as the comparisons of litter means, in which levels of variation were far greater.

Another factor that could potentially account for the negative findings of this study arises from the possibility that play behaviour could be subject to threshold effects (Martin & Caro 1985). Theoretically, it is possible that an individual must attain a certain threshold level of play before it can accrue *any* benefit from play, and if the whole study population fails to achieve such a level, individual variation in frequency of play would show no relationship with the outcome variables assessed in this study. However, it seems very unlikely that the study animals failed to attain a potential basal threshold of play since the study was conducted during a period of above-average rainfall (and high prey abundance) and levels of play were consequently high. Although it is conceivable that all members of the study population played more frequently than a theoretical upper level threshold of play (i.e. the level of play at which the maximum possible benefit is accrued), and this could potentially account for the lack of correlation between frequency of play and outcome variables, it seems implausible that such 'excessively' playful youngsters would still carefully tailor their rate of play to match their energy intake (Chapter 2) and, presumably, divert energy away from the lucrative benefits of growth (Clutton-Brock et al. 2001b), if no possible benefit were procurable from further play.

On a more practical level, the problems associated with any study of play behaviour did place a number of constraints on this study. Although working on a wild population provided numerous advantages and opportunities that are unattainable in captive studies, it also precluded the use of invasive manipulation experiments and thus limited the range of hypotheses that the study could assess. Finding a method to accurately and sensitively quantify individual differences in rate of play also proved extremely difficult. The relative rarity of play (even at its peak, in three-month-old animals, play occupied less than 6% of a meerkat's waking hours) precluded the use of instantaneous scan sampling (Altmann 1974) because an impossibly large sample was needed to document the relatively subtle differences between individuals. Similarly, focal animal sampling (Altmann 1974) was infeasible due to the highly sporadic and unpredictable occurrence of play (normally only a few minutes of highly intense play activity interspersed with hours of non-play), and it was not possible to guarantee 'all-occurrence' ad libitum sampling (Altmann 1974) when the whole group (up to 30 animals) was playing intensively. As a consequence, one/zero scan sampling (Martin & Bateson 1986) proved to be the most effective means of documenting rates of play, even though this methodology does not provide a true measure of frequency. Despite this, subsequent analysis revealed that the results obtained using one/zero scan sampling were not only closely correlated with those obtained from instantaneous scan sampling (for the seven litters of pups in which scans of both type were collected; Section 6.3.2), but also with the results of ad libitum sampling (i.e. number of play bouts) and, in hindsight, ad libitum sampling, despite its deficiencies during periods of intense play, would have been a more time-efficient means of quantifying rates of play.

Although play behaviour was unmistakable in meerkats over 4 weeks of age (due to the animal's stance and exuberant gait), object play (e.g. the pawing and mouthing of pebbles, vegetation, etc.) was frequently indistinguishable from exploratory behaviour in very small pups, whose movements are shaky and uncoordinated. Because of this ambiguity, it seemed wise to exclude pups of 3-4 weeks of age from most of the analyses undertaken by this study. A similar type of problem was encountered when attempting to document which individuals initiated play bouts, because the meerkats used cues so subtle (e.g. eye contact) that more than two-thirds of bouts appeared, to a human observer, to be mutually initiated. This imposed limitations upon how play partner preferences could be assessed.

10.3 SO WHY DO MEERKATS PLAY?

The obvious question that arises from the findings of this study is, 'Why *do* meerkats play?'. Clearly there are many hypotheses of function that were not assessed by this study (because of the difficulty of evaluating them in the field, or their limited relevance to the study species) and thus the answer to such a question must remain speculative. Nevertheless, several hypotheses can be discounted as highly unlikely.

10.3.1 Physical fitness

One of the hypotheses that is unlikely to account for the persistence of play behaviour in meerkats is that which suggests play functions to raise an individual's level of cardio-vascular fitness (Brownlee 1954; Fagen 1976, 1981) thus ensuring that it has the endurance it needs to cope with emergency situations (such as fleeing a threat). Such an outcome of play would be of great benefit to young meerkat pups, because they spend their first month of life pottering within 1-2 metres of their natal burrow, yet once they begin foraging with the group (normally at 28 days of age – Doolan & MacDonald 1996a) they often have to travel several kilometres in a day. Separation from the group (either because the pups lagged behind when the group moved quickly in response to a predator or an intergroup encounter, or because exhausted pups fell asleep at a bolt hole while the group was still moving) is a major cause of mortality in young pups (Russell et al. 2002). Clearly, if play functions to raise levels of physical fitness, there is good reason for meerkat pups to indulge in high levels of play during their time at the natal burrow, thus maximizing their chances of subsequently being able to keep up with their group. However, pups of this age played far less frequently than juveniles (Figure 6.1) – which rarely have problems keeping up with the group - and their frequency of locomotory play did not differ significantly from that of older pups which had been travelling with the group for a month or more.

10.3.2 Communication skills

Another hypothesis that seems improbable is that which proposes that play teaches young animals communication skills (Mason 1965; Dolhinow 1971; Jolly 1972; Poirier & Smith 1974). As observed in other species (Symons 1978b; Smith 1982), the play of young meerkats is conspicuously lacking in motor patterns derived from communication displays (whether visual, auditory or olfactory). Despite the species' rich and complex repertoire of alarm vocalizations (Manser et al. 2002), meerkats never uttered alarm calls playfully, and nor did they incorporate scent-marking behaviour (Gsell 2002) into their play. 'War-dancing', the highly conspicuous visual display which meerkats use to intimidate their adversaries during intergroup aggression was never observed in the play of wild meerkats, despite Wemmer & Flemming's (1974) observation of a "stiff-legged rocking gait' in their captive family. In fact, the behaviour most commonly adopted by meerkats to incite play was comprised of postures diametrically opposed to those adopted during displays of conspecific aggression, as postulated by Bekoff (1977c) and Spinka et al. (2001). For example, in the 'war-dance' display a meerkat jumps *forward* very conspicuously (or jumps and rocks to give the impression of forward motion even when remaining on the spot) with the head *stationary*, the mouth *closed* and the eyes fixed firmly on the opponent. In contrast, meerkats attempting to incite play use a gesture that consists of jumping or running *backwards*, with the head uplifted (nose pointing skyward), the mouth *wide open*, and the head *shaken* back and forth. Clearly, the exclusion of communicatory behaviour from play is not without purpose (eliminating the possibility of misinterpretation of intention), yet, under these circumstances, it seems most unlikely that a young meerkat could learn communication skills from play.

10.3.3 Telltale properties of play

One of the most striking features of mammalian play is that its behavioural composition varies from species to species (and even between the sexes within a species) in accordance with differences in serious adult behaviour patterns (Fagen 1981; Smith 1982). For example, the social play of meerkats very rarely includes stalking or pouncing, and object play (such as that shown by domestic kittens; West 1974) is almost entirely absent from meerkat play. This undoubtedly reflects the fact that meerkats feed primarily on subterranean invertebrates (Doolan & MacDonald 1996a) that require no 'hunting'. Traditionally, such taxa-specific (or sex specific) variations in play behaviour have been cited as evidence of play's role in the practice of adult motor skills (Smith 1982; Byers & Walker 1995), or, more recently, as verification that play has evolved to fulfill different functions in different taxa (Gomendio 1988; Bekoff & Byers 1998a). I would suggest that, on the contrary, this close association between the behavioural composition of play and the behaviours that a species finds most important, is evidence of a single, unitary function for all mammalian play.

Before exploring this claim further, it is important to note that not all species-typical behaviour patterns are incorporated into play. Meerkats, for example, never included digging behaviour in their play, even though digging is of immense importance to their survival. Meerkats not only dig to acquire their food (Doolan & MacDonald 1996a), but also to maintain their sleeping and breeding burrows (vital for surviving the desert's extreme temperatures) and the thousands of bolt holes they use to escape predators (Manser & Bell in press). So why don't meerkats incorporate this highly energetic motor behaviour into their play? It seems that meerkats, along with other mammal species, only integrate into play those motor patterns that the species has evolved to find stimulating and arousing; i.e. 'flight or fight' behaviours, such as mating, fighting, hunting or fleeing predators (Spinka et al. 2001).

A number of possible explanations for this ubiquitous trait have been proposed: for example, young animals may be using play to practice (or develop appropriate musculature for) rare but vital adult behaviours (Brownlee 1954; Smith 1982; Byers & Walker 1998), or, alternatively, they may be learning how to cope (physically and/or psychologically) with the life-threatening situations that arise during perilous 'flight and fight' behaviours (Spinka et al. 2001; e.g. falling while fleeing a predator, finding oneself in a disadvantaged position during a fight; Biben 1998). However, the behaviour of young meerkats does not lend support to these explanations. For example, although mounting behaviour is a common feature of meerkat play (occurring during 31% of all play interactions), copulation in meerkats is a thoroughly amicable affair in which a swat over the nose is the worst injury an animal will suffer (pers. obs.). Other species also incorporate non-life-threatening behaviours into play; for example, prey-catching motor patterns are prominent in the play of small felids (West 1974) but hunting is not a potentially dangerous activity for this group which prey almost exclusively on small rodents, birds and invertebrates (Leyhausen 1979). Similarly, if meerkats were undertaking mounting during play to practice the motor patterns used during mating, or to develop the appropriate musculature, female meerkats should not mount their playmates at exactly the same frequency as males (Section 9.4.3), since it is the males only that adopt this posture during copulation.

A more detailed examination of play behaviour, however, reveals that play does not only co-opt adrenal-related behaviour patterns, but any behaviour that markedly raises an individual's arousal and increases sensory (and motor) stimulation. For example, the inclusion of movements that stimulate an animal's vestibular system is another ubiquitous feature of mammalian play (Barber 1991). In the case of meerkats, such movements include exuberant leaping, rolling, twisting, wriggling and head shaking, but in other species they extend to dangling, bouncing, swinging, hanging upside-down and somersaulting (Barber 1991; Spinka et al 2001). The importance of this type of sensory stimulation to play in our own species is clearly evident from our playground equipment: from swings, slides and seesaws to round-a-bouts and roller coasters.

Similarly, it has long been recognized that novel objects or unusual substrates (e.g. loose straw, ice, mud, shallow water, etc.) tend to induce bouts of play (Wood-Gush & Vestergaard 1991; Spinka et al. 2001). In the case of meerkats, young pups encountering a tortoise for the first time will usually conclude their exploration with play (attempting to play fight while standing on the tortoise's shell). In a similar vein, a wide expanse of smooth, windblown sand (as occasionally develops on dune crests) has the power to halt a group of foraging meerkats and (during periods of abundant food) stimulate play fighting in all group members for anything up to an hour. Spinka et al. (2001) have suggested that this widespread phenomenon is a result of animals using play to learn to cope with unfamiliar stimuli (for example, learning how to adjust their gait or movements to handle the unfamiliar characteristics of the terrain). Unfortunately, this explanation does not appear to account for the behaviour of meerkats. No meerkat requires a knowledge of how to effectively mate or fight on the back of a tortoise, and pups only undertake play after their exploratory behaviour has revealed that the tortoise poses them no possible threat. Similarly, a species that spends its entire life on, in and under sand is unlikely to need to practice negotiating a substrate whose one novel characteristic is its total lack of impediments. I suggest that novelty stimulates arousal (because anything new could pose a threat) and (once the threat is negated) provides opportunities for new, and therefore exciting, sensory experiences. It is these two characteristics that make novel stimuli eminently suitable for incorporation into play. Meerkat pups discovering a tortoise are aroused by the possible threat of an unknown animal, and are provided with the sensory excitement of an elevated, slippery and moving platform for play fighting. Similarly, open expanses of sand stimulate meerkat play fighting because animals can attain an exuberance of movement (high speed chases, protracted rolling and tumbling, extravagant leaps) – and thus high levels of sensory stimulation - impossible to attain on sand that is vegetated with the Kalahari's typical barbed, thorned, burred or saw-edged plants.

If arousal and sensory stimulation are essential components of play, the widespread prevalence of social play (particularly play fighting), even in species that are solitary, becomes understandable. Considering that mammals have evolved a plethora of behaviours designed specifically to avoid physical conflict (from scent marking and vocalizations, to highly ritualized visual displays), the preponderance of play fighting, found in a huge number of species (Fagen 1981), is startling. However, as recognised by Biben (1998), play fighting provides an unparalleled level of tactile stimulation, which is intrinsically unpredictable and hence exciting. It seems likely that the tendency for young meerkats (Chapter 7), and many other species (Thompson 1998), to prefer well-matched partners during play is the result of animals attempting to maximize the unpredictability of a play fight's outcome and thus enhance its excitement.

10.3.4 Suggested function of play

Play behaviour appears to be tied intimately to a very diverse range of behaviours, movements and stimuli whose only commonality is that of heightened arousal and sensory stimulation. Why? We know that young rats provided with a stimulating environment develop heavier cerebral cortices (Rosenzweig & Bennett 1978), greater dendritic branching and neural connectivity (Ferchmin et al. 1970; Volkmar & Greenough 1972; Rosenzweig et al. 1978; Juraska et al. 1980) and better learning abilities (Rosenzweig & Bennett 1977) than littermates raised in an impoverished environment. And we know (from a series of experiments evaluating the components of environmental enrichment; Ferchmin et al. 1975, 1980; Ferchmin & Eterovic 1977, 1978) that this effect on cortical growth can only occur if three things are present concurrently: arousal, sensory stimulation and interactive behaviour (Rosenzweig et al. 1968; Bennett et al. 1979; Ferchmin & Eterovic 1982). We also know that the speed with which cortex weight increases in young rats is positively related to frequency of play (Rosenzweig et al. 1978; Ferchmin & Eterovic 1982), and that ontogenetic peaks in play coincide closely with periods of maximum cortex growth and differentiation (Suomi 1982). Play, unlike virtually all other behaviours, leads to a global activation of the cerebral cortex (Siviy 1998), as well as the widespread priming of an array of different neurochemical pathways (Siviy 1998). Based on this information, I would suggest that the function of play in young meerkats (and all other juvenile mammals) is to maximize growth and development of the cerebral cortex. Play not only provides the elements essential for the enhancement of cortical development (in fact, these elements are play's defining characteristics), but play behaviour is known to have a greater impact on cortex growth than any other apposite behaviour, such as exploration or formal training (Rozenweig et al. 1968; Bennett et al. 1979).

Although the majority of data currently available on play's effect on cortex growth is derived from the study of rats, it appears likely that the relationship is more widespread, with primates' brains responding to play in a similar manner (Gluck et al. 1973; Floeter & Greenough 1979). There is also a positive correlation between prevalence of play and relative brain mass, between taxa, in those groups that have so far been examined (e.g. Oretaga & Bekoff 1987; Byers 1999), and, of course, play is virtually non-existent in animals without a cerebral cortex (Fagen 1981). It should be noted, however, that the benefits of increased cortex weight and complexity are not yet certain, and while an improvement in learning ability seems very likely (Ferchmin & Eterovic 1982), the causality of the positive relationship between cortex weight and learning has yet to be established. It has also been suggested that play's global activation of the neurochemical systems that coordinate stress may improve the brain's ability to handle psychological stressors (Siviy 1998), potentially explaining why arousal appears to be an essential component of play.

10.3.5 Age distribution of play

I would suggest that the age distribution of play in meerkats (and in other mammal species) reflects the relative degrees of benefit (in relation to the enhancement of cortical function) and cost that are associated with play. Juvenile mammals, whose brains are actively growing, can clearly accrue large benefits from play (i.e. a permanent increase in cortex weight and, presumably, an enhanced facility for learning) and they will therefore tolerate relatively high costs. This explains why play is so widespread in juvenile mammals (Fagen 1981), why juvenile meerkats are willing to divert energy from growth into play (Chapter 2) and why many species are prepared to suffer an increased risk of predation or injury (Section 1.2.1) at a period in their lives when they are already highly prone to mortality (Gomendio 1988). Although the age profile of cortical development in young meerkats is not known, the peak period for play in this species coincides with the period of most rapid physical growth (White 2001), and this has also been observed in other taxa (Spinka et al. 2001).

As cortical growth slows, and the level of benefit derived from cerebral stimulation lessens, play tends to become less frequent. In many species, the approach of sexual maturity also increases the social risks of engaging in play (e.g. aggression, intimidation by dominant animals, reduced tolerance of adults) and, in some species, leads to the loss of trustworthy play partners through dispersal. With costs spiraling and benefits dwindling, many mammal species cease playing altogether. In meerkats, this period of increasing social hazard (and diminishing returns) appears to express itself (from around 6-7 months of age) as a decline in the frequency of play and a modification of the structural composition of play and partner preferences (Chapters 7 & 9) to minimize social tension. Nevertheless, the benefits of play are unlikely to disappear entirely, even in adults, because cortical stimulation facilitates and enhances neuronal connectivity and function (Kaczmarek 1993) and thus primes the brain for learning (which occurs most readily in an active brain - Siviy 1998). Meerkats are one of the few mammal species that continue to play as adults, and I would suggest that this is because their social organization keeps the costs of play unusually low. Delayed dispersal ensures that meerkats continue to have access to familiar, trusted partners, and the species' amicable intragroup relations (caused by a lack of benefit of rank within the natal group – Chapter 8) minimize the social risks of play. Similarly, the meerkats' highly cooperative reproductive behaviour, designed to cope with the harsh desert environment, frees individuals from the usual energetic constraints during periods of above-average rainfall.

10.4 CONCLUSIONS AND FURTHER RESEARCH

This study tested a number of previously unassessed explanations for the persistence of play behaviour in a small, social carnivore. The study found that none of these hypotheses was able to identify the fitness benefits that meerkats accrued from play. Such negative results are by no means unusual in the field of play research (Martin & Caro 1985) and this, combined with the fact that very few of the ecologically-based hypotheses of function can account for play in *all* taxa, has led to the belief that play is multi-functional (Gomendio 1988; Bekoff & Byers 1998a). However, I would suggest that since no study has found conclusive evidence of the function of play in even a single taxon (regardless of how profitable the hypothesized benefit would be to the species under study - e.g. social bonding in meerkats, or practice of hunting skills in cats – Caro 1980), a global mechanism (as yet untested) is likely to be responsible for play in all species; and such a benefit will almost inevitably be physiological.

Based on play behaviour's ubiquitous characteristics (age distribution, content, context, etc.), I believe that the physiological benefit most likely to be provided by play is the enhancement of the cerebral cortex (Ferchmin & Eterovic 1979, 1982; Fein 1982; Suomi 1982). This study was unable to evaluate this hypothesis because it was not amenable to testing in a wild population, using non-invasive means. While this hypothesized benefit of play is supported by our current knowledge of cortical development and function, it must remain speculative until further research is undertaken. Clearly, neurological studies are required to ascertain whether the relationship between play and cortical development observed in rats (and to a lesser extent in monkeys) also occurs in other taxa (including birds). We also need to identify the actual benefits provided by increased cortex weight, dendritic branching and neuronal connectivity, and establish whether the positive relationship that exists between cortex weight and learning ability is causal.

Further research is also needed to establish whether the distribution of play (with regards to age, sex and taxa) is consistent with predictions generated by hypothesis. For example, how closely do ontogenetic peaks in play behaviour coincide with ontogenetic peaks in cortical growth, in a range of taxa? And does the highly variable distribution of play observed between taxa, reflect taxa-specific differences in the cost/benefit ratio of play? For example, species in which 'quick wittedness' can provide tangible fitness benefits (e.g. cooperative hunters, social manipulators, opportunists, species caught in a predator/prey arms race, etc) would be expected to play more frequently as juveniles and be more likely to extend play into adulthood. Similarly, species in which the costs of play are unusually low (e.g. those living in harmonious social groups or aggregations, those freed from energetic constraints, etc) should also be more inclined to indulge in play. Sex differences in the play of mammals (where the females of many species play less than males as they approach maturity - Meaney et al. 1985) are likely to be caused by the heavier energetic constraints placed upon females by mammalian reproduction. This could be evaluated by comparing sex differences in the play of polygynous species with those of species in which males exhibit high levels of parental investment. Meerkats, of course, conform to this prediction, with males investing heavily in pup care (Doolan & MacDonald 1999) and the species showing no sex difference in rate of play (Chapter 6).

Finally, it is essential that experimental work be undertaken to compare the actual learning abilities of individuals that have enjoyed a play-enriched juvenile-period with those that have suffered depauperate play experiences (e.g. raised without same-aged peers, etc). I also believe that it is of considerable value to continue 'ruling out' the many untested ecological hypotheses of play's function through careful, systematic testing, using species for which the hypothesized benefit would provide strong selective advantages. Only through rigorous studies of this type will it be possible to ascertain whether play behaviour is multi-functionary.

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APPENDIX ONE

OTHER ASSOCIATED PUBLICATIONS

Behavioural tactics of breeders in cooperative meerkats.

Clutton-Brock, T. H., Russell, A. F. & **Sharpe, L. L.** 2004. *Animal Behaviour,* 68, 1029-1040.

Meerkat helpers do not specialize in particular activities.

Clutton-Brock, T. H., Russell, A. F. & **Sharpe, L.L.** 2003. *Animal Behaviour,* 66, 531-540.

Breeding success in cooperative meerkats: effects of helper number and maternal state.

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Cost minimization by helpers in cooperative vertebrates

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